Mechanistic understanding of climate-driven range shifts: using thermal tolerances of rock lobster to predict future change

By

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STATEMENTS AND DECLARATIONS

Declaration of Originality

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Statements of Co-Authorship

Chapters 2-5 of this thesis have been prepared as original research publications and have been/will be submitted to appropriate journals for peer review. The following people contributed to the manuscripts that form this thesis.

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GENERAL ABSTRACT

Climate change and ocean warming are driving changes in marine ecosystems globally. One of the most observed alterations are species' geographical re-distributions, or range shifts. Many of these shifts have been poleward extensions of species' ranges, however there is high variation in many aspects of these shifts. What causes these differences in species responses is likely complex and we currently do not have a strong understanding of the cause of this variation. Therefore, there is a pressing need to understand the mechanisms behind species' range shifts to be able to better predict future changes. One way to begin to understand what may cause a species to shift their range is to investigate their physiological and behavioural thermal tolerances. Here, the thermal tolerances of a range of performance measures of a local and a range-shifting species of spiny lobster in south-east Australia were explored, and potential responses of both species to future ocean warming in the region were modelled. Eastern rock lobster, *Sagmariasus verreauxi*, are a large species of spiny lobster found along the east coast of Australia and are suspected of undergoing a range shift further into Tasmanian waters, currently occupied by the resident species, southern rock lobster, *Jasus edwardsii*. The effect of this range-shifting species and its potential interaction with the local species has implications for the valuable local commercial *J. edwardsii* fishery, as well as for the marine ecosystem in Tasmania. Understanding potential mechanisms behind species' range shifts is key to being able to predict future changes and proactively manage resources sustainably.

Thermal performance curves allow exploration and visualisation of how a species' measure of performance changes with temperature. Thermal performance curves of multiple measures of performance for the two species of lobster, *J. edwardsii* and *S. verreauxi*, at two different life stages, puerulus (final larval stage) and juvenile, were investigated. Using intermittent-flow respirometry, the effects of temperature on aerobic metabolism and aerobic scope across the temperature gradient were developed into thermal performance curves. The effect of

temperatures on escape speed, an important survival performance measure, was also measured. It was found that the two species have different thermal tolerances between multiple measures of performance as well as between life stages. This suggests that a single measure of performance may not accurately be able to predict whole-organism changes under ocean warming scenarios.

To further determine whether individual species' thermal tolerances can be used to predict changes to species' interactions under ocean warming scenarios, competitive trials for food resources between the two lobster species over a range of temperatures were conducted. Single adult individuals of both species were placed in a tank with a single food item and the resulting interaction filmed for analysis. *Jasus edwardsii* was successful in obtaining the food item before *S. verreauxi* in the majority of trials. *Jasus edwardsii* also exhibited significantly more aggressive behaviours than *S. verreauxi*, who exhibited significantly more submissive behaviours over the temperatures range tested. These results indicate that *Jasus edwardsii* is competitive at and above temperatures determined optimal for other performance measures in previous studies. It also suggests that while individual thermal tolerances are valuable measures for individual performance under changing climate conditions, they may not be sufficient in predicting changes to the outcomes of interactions due to unforeseen indirect effects in terms of organism behaviour.

To gain a more comprehensive understanding of how populations may react to changing ocean conditions, modelling approaches can be used to investigate aspects of species performance not readily obvious from experimental results. Models of Intermediate Complexity for Ecosystem assessments (MICE) are flexible, targeted models that can be used to answer specific questions such as; how will a range shifting lobster affect a resident species in Tasmania? The two-part model first explores how individual physiological thermal tolerances affect projected biomass under a range of scenarios, and secondly incorporates competitive

interactions into the framework to project changes as a result of indirect effects of ocean warming. From part one of the model, population trajectories that incorporated physiological data into the model greatly changed the projected biomass. *Jasus edwardsii* projected biomass remained stable or increased slightly over the 50-year projection, while *S. verreauxi* biomass is projected to greatly increase, a result consistent with their thermal tolerances and future projected ocean warming in the region. Incorporating competitive interactions in the second part of the model changes the dynamics due to the two populations sharing resources. In these projections, *J. edwardsii* projected biomass decreased, while *S. verreauxi* projected biomass increased. Here, it is assumed that the effects of thermal tolerances of the two species outweighs the increased competitive ability of *J. edwardsii* over *S. verreauxi*. These results show that incorporating thermal tolerance data into models can greatly affect the outcome of the projections, and that indirect effects of climate changes such as those to species interactions may have considerable effects on populations with potential knock on effects for marine ecosystems.

These results all indicate that the mechanisms facilitating or hindering species range shifts are complex and not always easily apparent. While predictions about individual species performance under climate change may be relatively simple to develop, the ability to predict changes to marine communities or ecosystems is much more complicated. Here it is shown that a wide range of techniques can be used to aid in our pursuit for greater understanding of species' range shifts and their potential effects on marine communities. Ultimately, a comprehensive framework is required that incorporates both experimental and modelling techniques to best grasp current and future changes to both individual species and marine ecosystems.

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CHAPTER 1

General Introduction

Introduction to species' range shifts

Climate change is affecting marine environments worldwide, with global trends of increased ocean temperature, acidification and sea level rise, and changing ocean circulation affecting marine ecosystems at local and regional scales (Hoegh-Guldberg & Bruno 2010, Doney et al. 2012, IPCC 2014). However, these effects of climate change are not being felt equally. There is regional variation in all elements of marine climate change, including temperature, oxygenation, pH, currents, and stratification. In some localised areas, such as south-east Australia, ocean warming is occurring at rates 2-4 times faster than the global average rate, creating hotspots globally where climatic-induced changes to species and communities may be accelerated (Frusher et al. 2014, Hobday & Pecl 2014, Pecl et al. 2014). Temperature changes are of particular importance to marine ectothermic species, whose body functions and life history are temperature-dependent through their physiology (Pörtner & Knust 2007, Pörtner & Farrell 2008, Bozinovic & Pörtner 2015). Changes in physiology due to changes in temperature can affect behaviour and performance, ultimately determining survival, growth, reproduction and overall fitness of individuals.

As a result of ocean warming, many marine species are altering their geographical distribution to either escape temperatures exceeding their thermal preferences or to exploit environments previously closed to them (Parmesan & Yohe 2003, Hoegh-Guldberg & Bruno 2010). Changes to species' distributions have been observed from tropical to polar regions and encompass fish, invertebrates and habitat-forming species (Parmesan & Yohe 2003, Pitt et al. 2010, Last et al. 2011, Wernberg et al. 2011, Poloczanska et al. 2013, Vergés et al. 2014). The most common trend currently observed is the poleward extension of species' distributional range boundaries (Parmesan & Yohe 2003, Poloczanska et al. 2013). While species' range shifts are a global phenomenon, understanding what changes are happening regionally is a key step in identifying drivers of species' range shifts.

South-east Australia, identified as an ocean warming hotspot with long-term rates of warming almost four times the global average, has observed many range shifts of species (Hobday & Pecl 2014, Pecl et al. 2014). This increased rate of warming is due to a strengthening and extension of the East Australian Current pushing further south into Tasmania (Ridgway 2007). This extension has brought with it tropical and sub-tropical species to locations further south than they would usually be seen (Booth et al. 2007, Ridgway 2007, Figueira et al. 2009, Ling et al. 2009, Johnson et al. 2011). With the elevated water temperatures, tropical species are able to overwinter in cool temperate areas after they have been transported, enabling them to exploit a new environment and establish new populations (Booth et al. 2007, Figueira et al. 2009). One example of a range-extension that was facilitated by the extension of the East Australian Current is the range shift of the long-spined urchin, *Centrostephanus rodgersii*, into Tasmanian waters where it has since overgrazed many of the kelp forests in Tasmania and is continuing to create urchin barrens (Ling et al. 2009, Johnson et al. 2011).

However, not all range extensions of species into south eastern Australian waters have been as obvious and detrimental as the urchin. A study from the south-east coast of Tasmania revealed that intertidal and subtidal invertebrates have made poleward expansions of their range limits at a rate of approximately 29 km decade^{-1} (Pitt et al. 2010). One species of barnacle not present in Tasmania in the 1950's, the giant rock barnacle, *Austromegabalanus nigrescens*, is now common along the east coast (Pitt et al. 2010). Another study from the same region found 61 species from 37 families of temperate reef fish have exhibited significant compositional changes over a time period spanning from the 1890's to recent years (Last et al. 2011). Of these, 45 species (74%) showed distributional changes thought to be climate-related. A regional meta-analysis from the Tasman Sea found 104 species (51 species of fish, 53 species of invertebrates) that exhibited poleward range extensions with an average of 24.1 ± 87 km for all species and 37.7 ±69.6 km for fish species (Sunday et al. 2015). In addition to range extensions, there have

also been accounts of range contractions. Of particular importance in Australia, the Tasmanian giant kelp, *Macrocystis pyrifera*, and Western Australian kelp, *Ecklonia radiata*, among other seaweeds, have been observed contracting their ranges in response to ocean warming (Johnson et al. 2011, Wernberg et al. 2011).

There have been a range of studies to identify factors that can be used to explain the variation in species' climate-driven range movement. Climate velocity, or how fast and in which direction ocean changes are happening, has been shown to explain a significant amount of variation in species' responses and also to be able to predict species' range movement (Pinsky et al. 2013, Burrows et al. 2014, Sunday et al. 2015). Species' traits, such as dispersal ability, trophic position and body size, have shown differing strengths in explaining variation in responses to climate change. Some studies have shown species' traits are able to explain much of the variation observed (Sunday et al. 2015) and also help predict tropical vagrancy (Feary et al. 2014). Other studies, however, indicate that species' traits do not explain variation significantly (Pitt et al. 2010, Pinsky et al. 2013). While species' range movement is a global phenomenon, there is a large amount of variation in terms of directions and magnitudes of observed range changes and these correlative studies are not able to fully explain this variation. Developing a more mechanistic understanding of species' range shifts using aspects of physiology may be critical to understanding the drivers of species' range shifts, allowing more accurate predictions for future changes in the oceans.

There are many factors that may affect species and their ability to shift in response to climate change. These range from direct effects, such as effects of temperature on species' individual physiologies, to indirect effects that arise due to complex species interactions. While these factors and processes are important in facilitating or hindering species' range shifts, this thesis focuses on only a few of these aspects, including the effect of temperature on specific physiological traits and competitive interactions.

Thermal effects on physiological performance

Climate change directly affects species by altering the physical environment they live in. As many marine species are ectothermic, their internal physiology is highly dependent on ambient conditions and is a main determinant of how a species functions and behaves (Pörtner & Knust 2007, Pörtner & Farrell 2008, Doney et al. 2012, Bozinovic & Pörtner 2015). Even small physical changes, as little as a 1°C increase in water temperature, has the ability to cause large disruptions to species' physiology and life history (André et al. 2009, Hoegh-Guldberg & Bruno 2010). With increasing ocean temperature, rates of species' body functions, such as metabolism, growth and body velocities, are likely to change, with impacts on species' performance, phenology and behaviour.

One way to investigate the effect of changing temperature on measures of species' performance is to use thermal performance curves (Figure 1.1). Thermal performance curves can be used to illustrate the effect of temperature on many physiological processes such as metabolism, growth rates, reproduction and escape speeds (Eme & Bennett 2009, Dell et al. 2014). Determining optimal or sub-optimal temperatures for different measures of species' performance may allow us to determine which biological factors may facilitate or hinder a species' ability to shift its range in response to ocean warming.

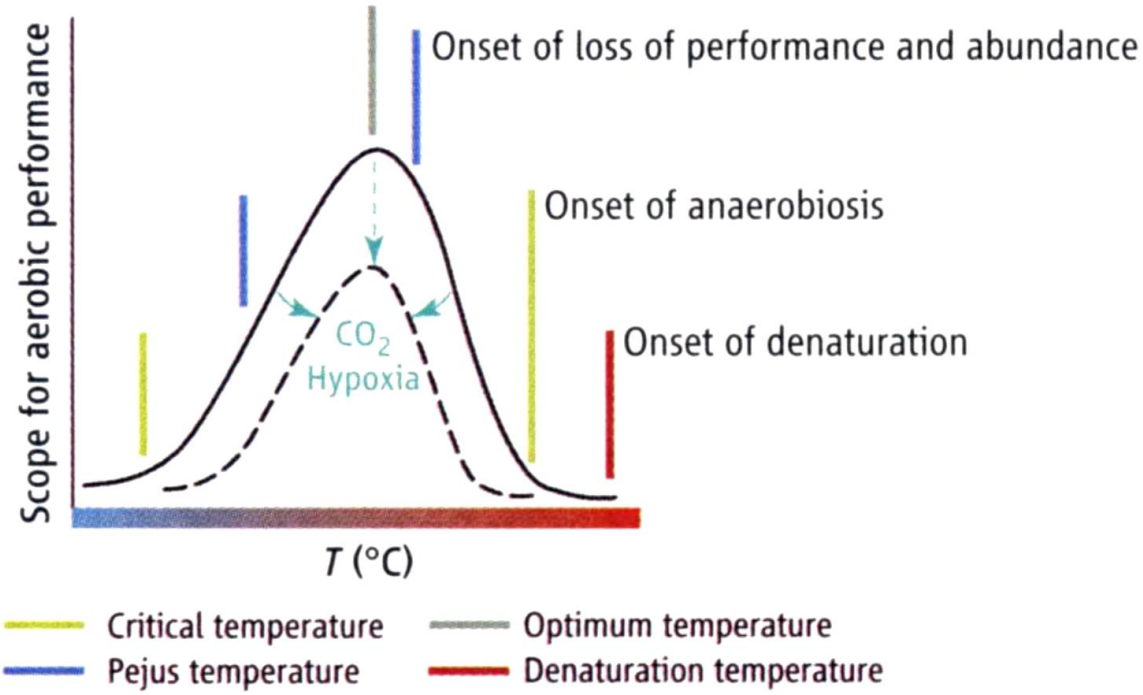

Figure 1.1. Thermal performance curve, with indicators of optimal, pejus and critical temperatures for a measure of species' performance, in this case aerobic performance. Figure from Pörtner and Farrell (2008).

Aerobic metabolism

A common, yet currently controversial, measure of physiological performance used to investigate effects of temperature on ectothermic species is aerobic scope (Fry 1947, Fry & Hart 1948). Aerobic scope is the difference between maximum and resting metabolic rates and can provide an indication of the amount of energy available for non-essential body processes, such as growth and locomotion. The oxygen and capacity-limited thermal tolerance hypothesis proposes that there is a limited thermal range for individual ectothermic species in which performance, measured as aerobic scope, is maximised (Pörtner & Knust 2007). This optimisation, and subsequent decline in performance at temperatures outside of this optimal range, is hypothesized to be due to the mismatch between oxygen demand and supply (Pörtner & Knust 2007). This measure of organismal performance has been proposed as a way to predict

future changes in species' population characteristics under climate change (Pörtner & Farrell 2008). However, there is increasing evidence from recent studies that indicate that aerobic scope may not be sufficient to predict whole-animal performance (Norin et al. 2014, Fitzgibbon et al. 2017, Jutfelt et al. 2018). Different organismal processes have different responses to increases in ambient temperatures, such as the difference between growth rate optimums and aerobic scope in juvenile eastern rock lobster *Sagmariasus verreauxi* (Fitzgibbon et al. 2017) and different thermal optima for feeding and growth performance in juvenile barramundi, *Lates calcarifer* (Katersky & Carter 2007). Moreover, aerobic scope is unable to predict thermal preference or performance in juvenile barramundi, *L. calcarifer* (Norin et al. 2014). However, while aerobic scope may not be a universal proxy for performance, it has the potential to be highly valuable metric for understanding the effect of temperature on energetic performance (Clark et al. 2013).

Escape performance

Another measure of performance that provides a different ecological insight is escape speed. Ocean warming will affect escape performance of marine ectotherms through changes in muscle performance, burst swimming speed and acceleration (Johnson & Johnston 1991, Bailey & Johnston 2005, Dell et al. 2011, 2014, Schalkhausser et al. 2014). With predicted warming, some species may increase their swimming performance whiles others living close to their thermal limits may experience a decline (Dell et al. 2014). As attack and escape performance are key factors in the outcome of predator-prey interactions, the effect of ocean warming on performance may have far reaching effects on marine community structure (Cairns et al. 2008, Grigaltchik et al. 2012, Dell et al. 2014, Ohlund et al. 2015).

Burst swimming is seen through all stages of life in many marine organisms, from larval stages through to adults. This is an important factor for many species' as their burst swimming performance can determine their survival in predator-prey interactions. However, with

warming, it is unlikely two species in an interaction will react the same way to changes in temperature, resulting in asymmetries in their respective performance and hence the outcome of the interaction (Grigaltchik et al. 2012, Dell et al. 2014). Studies investigating the effects of temperature on escape speeds have found high variation in species' responses. For example, there are species that exhibited no significant effect of temperature on their escape performance, e.g. the long-spined sea scorpion, *Taurulus bubalis*, was not visibly affected by increased temperature, showing no changes in body velocity even after a period of thermal acclimation (Temple & Johnston 1998). In contrast, there are species that showed increased swimming performance with warming e.g. swimming velocities of larval herring, *Clupea harengus,* and plaice, *Pleuronectes platessa*, were strongly temperature dependent, as tail beat frequency increased from 18 beats per second at 5°C to 35 beats per second at 15°C (Batty & Blaxter 1992). In addition, the short-horn sculpin, *Myoxocephalus scorpius*, after a period of acclimation to higher temperatures, recorded faster length-specific velocities and improved escape performance (Temple & Johnston 1998). There are also species that show declines in swimming performance with increasing temperatures. For example, in adult Pomacentrids, swimming performance is sensitive to a relatively small increase in ambient temperature from 29°C to 32°C, where 10 species of damselfish all showed decreases in body velocity, though to varying degrees (Johansen & Jones 2011). This variation in species' escape response indicates that it is a complicated survival process and is likely dependent on individual thermal tolerances and predation pressures in the community.

Thermal effects on species' interactions

Species' range shifts also have the capacity to alter inter-specific interactions, such as predator-prey or competitive interactions for resources, in multiple ways (Kordas et al. 2011, Dell et al. 2014, Lord et al. 2017). As temperatures change, so will species responses and it's unlikely

two interacting species will react to temperature changes in the same way (Figure 1.2). For example, two species may have different magnitudes or rate of response to changes in temperature, resulting in a mismatch of performance between the species (Figure 1.2). It is also likely that two interacting species will have different thermal optimums for the same performance measure, potentially resulting in a new, novel species' interactions where new species exploit regions with existing communities in new thermal environments, creating new interactions with the resident species (Johnson et al. 2011, Marshak & Heck 2017). Likewise, many current species' interactions are likely to be modified or eliminated with changes in species' ranges or abundances, altering individual performance of one or both species (Milazzo et al. 2013). It is unlikely that both species in an interaction will react to changes in temperature in the same way, hence asymmetries will arise in the response and outcomes of interactions (Grigaltchik et al. 2012, Dell et al. 2014, Figure 1.2). Changes to species' interactions have implications for the structure and function of marine ecosystems and understanding these are critical to be able to effectively predict future changes.

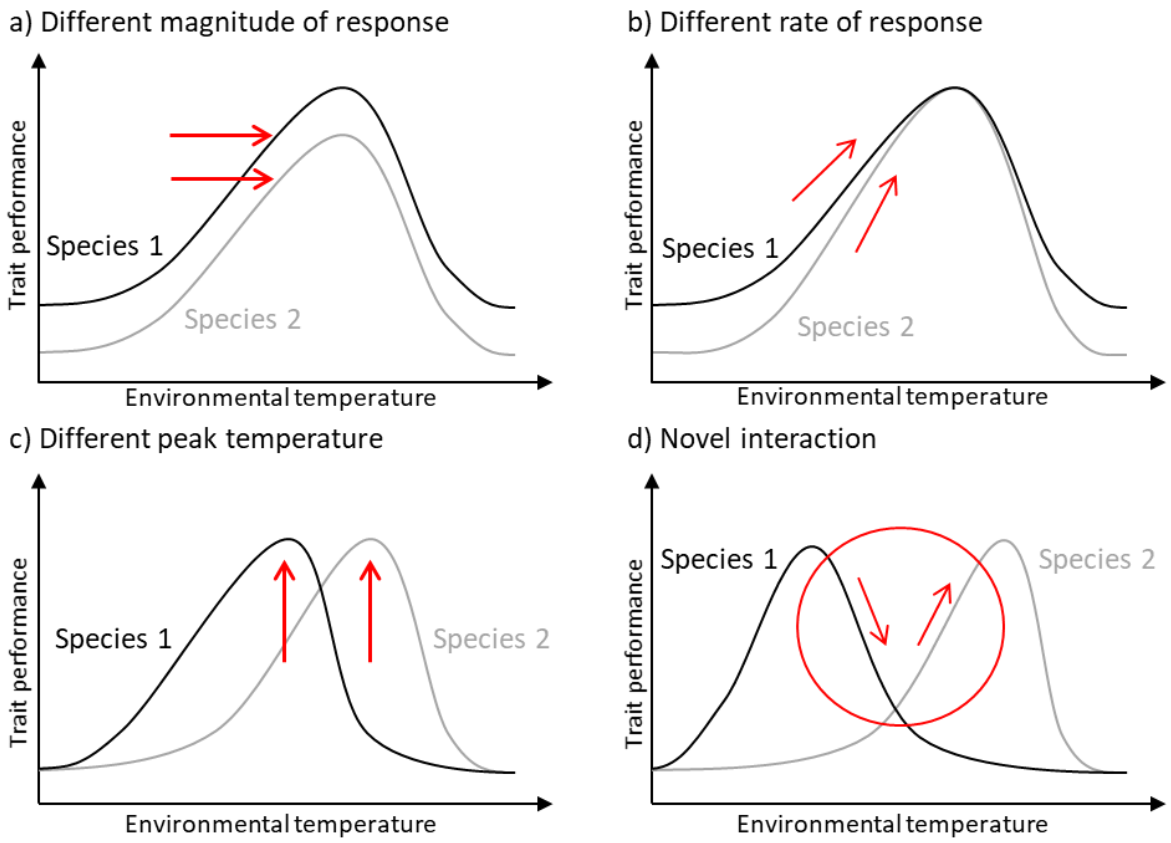

Figure 1.2. Different responses of interacting species performance measures as a result of climate change, where a) shows different magnitudes of responses by two interacting species, b) different rates of response between two species, c) different peak temperatures between two species and d) a new, novel interaction between two species. Figure adapted from Dell et al. (2014).

Competitive interactions

Competition between species for resources is a major structuring influence on marine communities (Dayton 1971). Changes to these interactions via species' range shifts has the potential to alter marine ecosystems directly and indirectly (Kordas et al. 2011, Milazzo et al. 2013). For example, the competitive ability of a warm-water wrasse species, *Thalassoma pavo,* is expected to increase with ocean warming while its cold-water species counterpart *Coris julis* is expected to decrease in competitive performance as an indirect consequence of the increase in performance of *T. pavo* (Milazzo et al. 2013). Competition between three species of sculpin in Greenland is also likely to change with ocean warming, where the warmer water species is

able to outcompete the cooler water species for shelter (Seth et al. 2013). Changes to species' dominancy is also a result of species' range shifts and altered competitive performance, and can affect fisheries. For example, the small pelagic fishery of south-east Australia where catches shifted from jack mackerel, *Trachurus declivis*, to redbait, *Emmelichthys nitidus*, as a result of changes in prey species (McLeod et al. 2012).

While direct effects of ocean climate change are usually the most visually obvious, it is becoming increasingly clear that indirect effects as a result of changing species' interactions are more important in the structure and function of marine ecosystems (Kordas et al. 2011, Kroeker et al. 2014, Lord et al. 2017). Using thermal performance curves may help identify how individual species in an interaction may react to changes in ocean temperatures and potentially inform at what temperature a change in the expected outcome of a species' interaction may occur. However, as alterations to species' interactions in a warming environment can be complex and unpredictable, using thermal performance curves may not be enough alone. Investigating the effects of temperatures on species' interactions directly may provide insights that would not be gained from using individual species' performance curves. In addition, incorporating physiological data such as thermal performance curves into mechanistic models may elucidate some of the less intuitive changes we may see in marine ecosystems.

Spiny lobsters

Lobsters play an important role in communities as both predator and prey species (Butler et al. 2006). They also have among the longest and most complex larval life cycles of any marine invertebrate, lasting for up to two years in some species with this stage being important for dispersal, and possibly range extensions (Figure 1.3, Phillips et al. 2006). These early life stages

may also be more susceptible to effects of climate change and ocean warming than their juvenile and adult counterparts (Pörtner & Farrell 2008, Storch et al. 2011, Fitzgibbon et al. 2014b). The puerulus stage of the spiny lobster life cycle is a critical transitional stage from pelagic larvae to recruitment into the juvenile population (Figure 1.3). It is a nektonic, non-feeding stage that actively swims to settle onto suitable habitat substrate in coastal regions (Fitzgibbon et al. 2014a). Like many larvae settling into new communities, puerulus must survive the 'wall of mouths', where there is higher predation pressure on these new recruits trying to settle into their new environment (Emery 1973, Hamner et al. 1988). Physiological performance, such as escape speed, is critical for survival for puerulus stage lobsters and changes to these measures with warming may have far-reaching effects for the local and potentially range-shifting population.

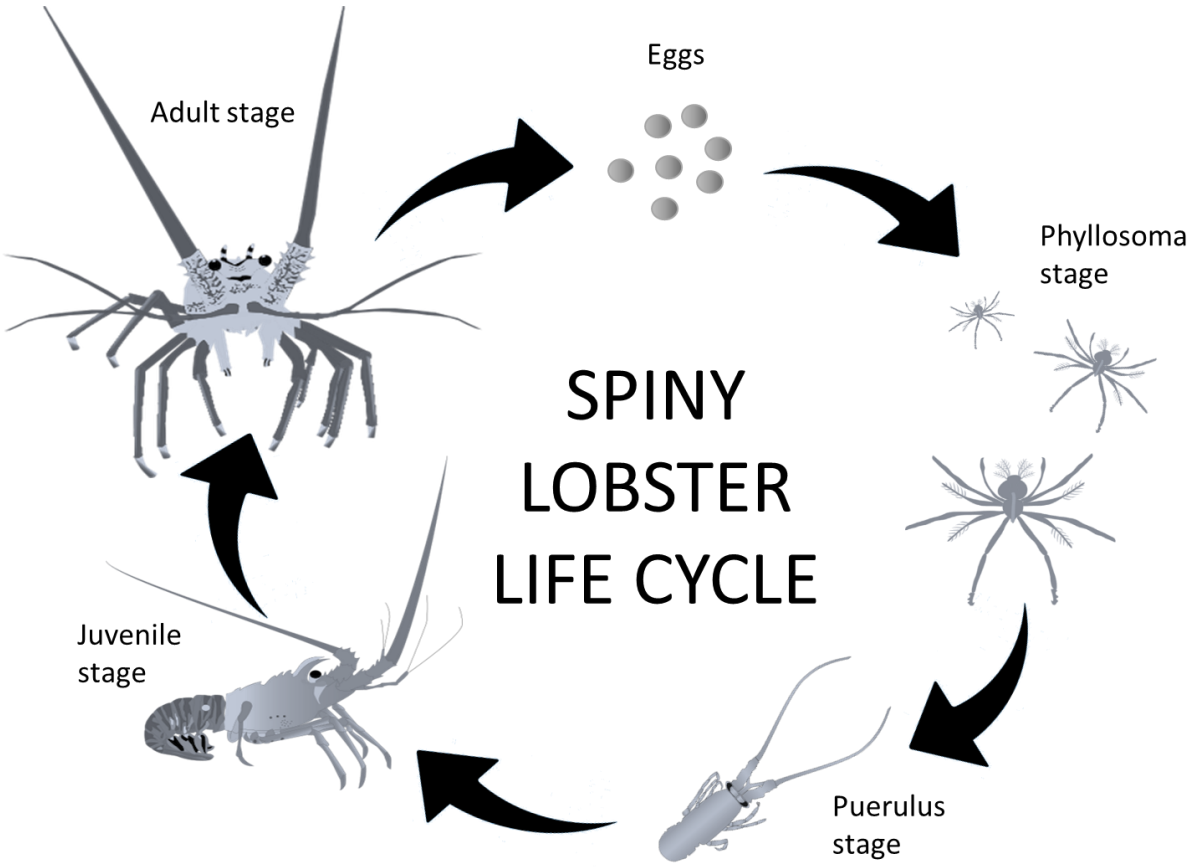

Figure 1.3. Spiny lobster life cycle. Images courtesy of the Integration and Application Network, University of Maryland Centre for Environmental Science (ian.umces.edu/symbols/).

Southern Rock Lobster

Jasus edwardsii (Hutton 1875), commonly known as southern rock lobster, are found along the southern coast of Australia, from south-west Western Australia, east to Victoria and south into Tasmania, as well as around New Zealand (Figure 1.4). It is a highly valuable species ecologically, economically and socially (Pecl et al. 2009, Plagányi et al. 2018). *Jasus edwardsii* is a known predator of the range-extending and barren-forming urchin, *C. rodgersii* (Ling 2008, Redd et al. 2008, Johnson et al. 2011). In marine reserves where numbers of larger lobsters are higher, predation occurs at a higher rate and the marine environment exhibits resilience to the influx of urchins (Ling & Johnson 2012). It also forms one of the most valuable commercial fisheries in Tasmania, as well as being an important recreational target species (Pecl et al. 2009, Plagányi et al. 2018).

Eastern Rock Lobster

Sagmariasus verreauxi (H. Milne Edwards, 1851), commonly known as eastern rock lobster, are found along the east coast of Australia between southern Queensland and northern Tasmania, as well as off New Zealand (Figure 1.4). *Sagmariasus verreauxi* is the largest species of spiny lobster in the world, growing to 242 mm carapace length (Montgomery 1992). It also forms another valuable fishery in New South Wales where it exported as a valuable seafood commodity as well as being a valuable recreational species (Montgomery et al. 2009, Plagányi et al. 2018). This species is also thought to be a predator of *C. rodgersii*, however, information regarding its feeding ecology is lacking (Byrne & Andrew 2013).

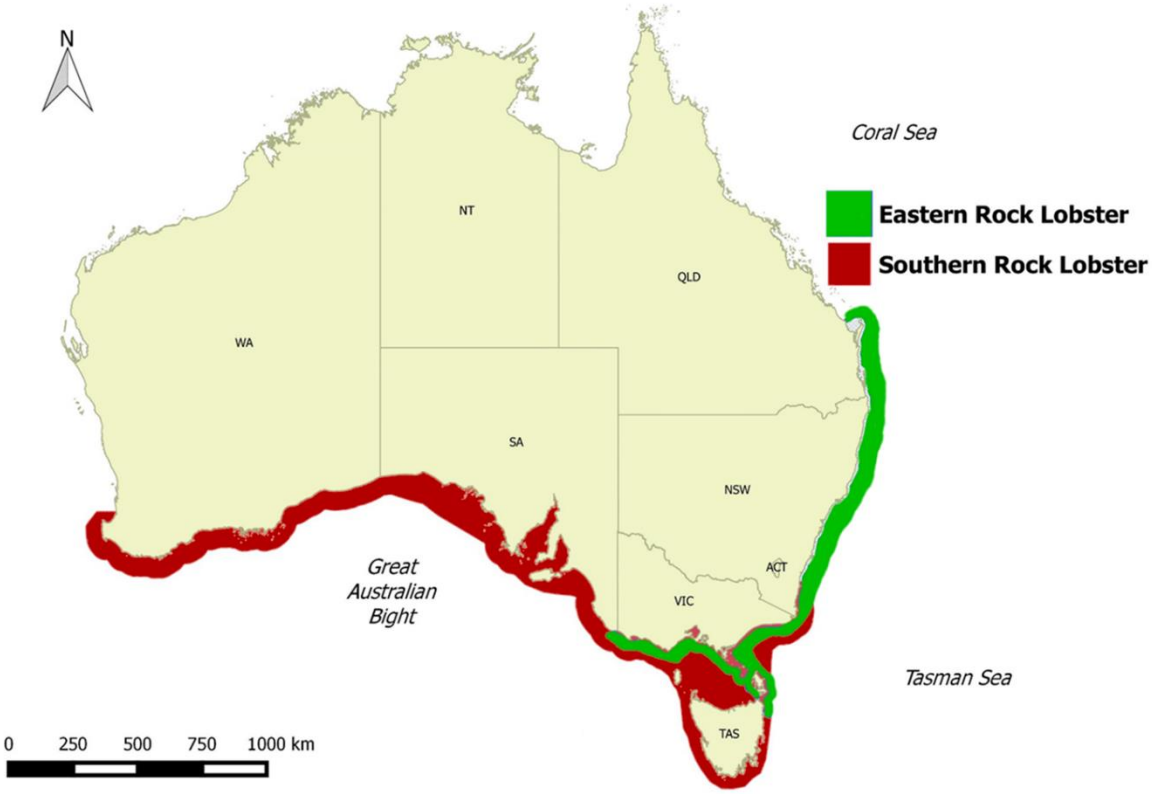

Figure 1.4. Map of eastern rock lobster, *Sagmariasus verreauxi*, and southern rock lobster, *Jasus edwardsii* distributions in Australia. Map by C. Villanueva.

Thesis rationale, aims and structure

While there have been many studies documenting species' range shifts, we still lack a mechanistic understanding of why species are shifting at different rates and magnitudes and impacts on the biological communities into which they move. It is important to understand what drives or facilitates these shifts to be able to predict future changes and adaptively manage marine resources sustainably. Here, the thermal tolerances of two species of spiny lobster were investigated in an attempt to identify factors that may facilitate or hinder species' ability to shift and how that shifting species may interact with other species in its new community. While historically *S. verreauxi* has been found intermittently along the northern coast of Tasmania, it is currently suspected of undergoing a range shift down the Tasmanian east coast (Robinson et al. 2015). This potential range shift has implications for both fisheries and ecological

management. While not currently a targeted fisheries species in Tasmania due to low abundance, continued ocean warming and increased *S. verreauxi* recruitment may facilitate a new lobster fishery, or *S. verreauxi* may compete with the more valuable existing southern rock lobster fishery (*J. edwardsii*) in the region. Understanding how these two species will react to ocean warming and each other is critical to predict future changes and inform sustainable management of both species.

The aim of this thesis is to develop a mechanistic understanding of species' range shifts by investigating the thermal tolerance of potential physiological mechanisms and competitive interactions that may facilitate or hinder range shifts and modelling the effect of these factors to project future changes in populations of both *J. edwardsii* and *S. verreauxi* in Tasmania.

This thesis consists of this general introduction, three chapters reporting on experiments, one modelling chapter and a general discussion. As each of the experimental data and modelling chapters are written (and submitted) as research articles, some repetition exists in the Introductions of these chapters. Due to the integrating nature of the modelling chapter in terms of drawing general conclusions based on the first three chapters, the general discussion is relatively short to minimise overlap.

This introductory chapter (Chapter 1) provided the background for the research in subsequent chapters and highlights the current knowledge gaps.

Chapter 2 investigates the thermal tolerances of multiple performance measures on puerulus stage *S. verreauxi*, the final larval stage of a range-shifting species of spiny lobster.

Chapter 3 expands on the study in chapter 2 and investigates the thermal tolerances of multiple species' performance measures at multiple life stages of *J. edwardsii* and *S. verreauxi* in Tasmania.

Chapter 4 investigates the effect of increasing temperatures on the competitive interaction between *J. edwardsii* and *S. verreauxi*.

Chapter 5 develops a Model of Intermediate Complexity for Ecosystem assessments (MICE) using physiological and competitive thermal tolerance data from chapters 2-4 to project population biomass changes in *J. edwardsii* and *S. verreauxi* along the east cost of Tasmania under future ocean warming scenarios.

Chapter 6 synthesizes results of the experimental and modelling chapters and provides direction for future research.

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CHAPTER 2

Multiple measures of thermal performance of early stage Eastern rock lobster in a fast-warming ocean region.

In review in Marine Ecology Progress Series

Abstract

To date, many studies trying to understand species' range shifts have each focused on a single potential mechanism. While a single mechanism may give some insight, it may not be enough to accurately predict outcomes. Here, multiple measures of performance are used to explore potential mechanisms facilitating or hindering species range shifts. The thermal pattern for multiple measures of performance, including measures of aerobic metabolism and multiple aspects of escape speed, using the final larval stage (puerulus) of eastern rock lobster, *Sagmariasus verreauxi*, as a model species, was examined. Aerobic scope and escape speed were found to have different thermal performances and optimal temperatures. The temperature at which aerobic scope was maximised was ~27°C, while the temperature at which maximum escape speed was maximised was ~23°C. This discrepancy in thermal performance indicators illustrates that one measure of performance may not be sufficient to accurately predict whole animal performance under future warming. Time taken to recovery and excess post-exercise oxygen measurements increased exponentially with temperature, indicating increased costs at higher temperatures. Using multiple measures of performance and appropriate modelling techniques may lead to a more accurate prediction of future range shifts, including the timing and extent of redistribution.

Keywords: *climate change, aerobic scope, escape speed, respiratory metabolism, crustacean larvae, puerulus,* Sagmariasus verreauxi.

Introduction

Ocean warming is affecting marine species worldwide (Pecl et al. 2017). One of the most prevalent effects observed are changes to species' geographical distributions (Sunday et al. 2012, Poloczanska et al. 2013). While these 'range shifts' occur in many marine systems, we do not yet have a clear understanding of the mechanisms driving the high variation in rate and magnitude of these changes within (Last et al. 2011, Sunday et al. 2015) and between regions (Poloczanska et al. 2013). Part of the explanation may lie in the complex physiology of marine species and how each aspect of their physiology reacts to changes in their thermal environments.

Many marine species are ectothermic, meaning that their internal physiology is highly dependent on ambient temperature which in turn strongly influences species function and behaviour (Pörtner & Knust 2007, Pörtner & Farrell 2008, Doney et al. 2012). To understand the effect of temperature on many physiological and biological processes, thermal performance curves can be constructed. Thermal performance curves allow visualisation of the effects of temperature on bodily rates such as metabolism, growth and reproduction (Eme & Bennett 2009, Dell et al. 2014, Donelson et al. 2014). With increasing ocean temperatures, bodily rates are likely to change due to heightened metabolic performance, with consequent effects on species performance and behaviour. While single thermal performance curves may provide some insight to how a particular body function may change under ocean warming, it may be of limited use as a predictor of whole animal performance.

Aerobic scope, a proxy for the amount of energy available for non-essential body processes, is a key component of organismal energy budgets and is dependent on ambient temperature experienced by ectotherms (Watson et al. 2014). The oxygen and capacity-limited thermal tolerance hypothesis proposes that there is a limited thermal range for individual ectotherm species in which performance, measured as aerobic scope, is maximised and has been proposed as a way to predict future changes in species population characteristics under climate change

(Pörtner & Knust 2007, Pörtner & Farrell 2008). However, while aerobic scope is a valuable measure of performance, there has been an increase in the number of studies that suggest that aerobic scope is an incomplete measure of whole-organism performance and hence a predictor for future changes (Norin et al. 2014, Fitzgibbon et al. 2017, Jutfelt et al. 2018). Different organismal processes have different responses to increases in ambient temperatures, such as the difference between growth rate optimums and aerobic scope in juvenile eastern rock lobster *Sagmariasus verreauxi* (Fitzgibbon et al. 2017) and different thermal optima for feeding and growth performance in juvenile barramundi *Lates calcarifer* (Katersky & Carter 2007). Moreover, aerobic scope is unable to predict thermal preference or performance in juvenile barramundi (Norin et al. 2014).

To gain a more robust understanding of the effects of climate change on marine communities we need to incorporate measures of species interactions, such as competition or predation performance along with this individual physiological performance data (Evans et al. 2015). Another potential constraint, or conversely, facilitator, to species range change under ocean warming are inter-specific interactions. Changes to a species' individual physiology under climate change are also likely to influence its interactions with other species, by modifying or eliminating current interactions or creating new ones (Pitt et al. 2010, Kordas et al. 2011, Pinsky et al. 2013). For example, predation plays a critical role in structuring and functioning of marine communities as predator-prey interactions provide a link for transfer of energy, nutrients and materials from basal species to apex predators (Paine 1974, Dell et al. 2014). Predator-prey interactions are affected by temperature through effects on active body velocity in ectotherms (Grigaltchik et al. 2012, Dell et al. 2014). As attack and escape performance are key factors in the outcome of predator-prey interactions, the effect of ocean warming on ectotherm mobility and locomotion may have far reaching effects on marine community structure (Cairns et al. 2008, Dell et al. 2014, Ohlund et al. 2015).

The south east coast of Australia has been identified as an ocean warming hotspot, where rates of warming are up to four times the global average (Hobday & Pecl 2014, Pecl et al. 2014). In recent years, Australia has seen many changes in the distribution and abundance of local species as well as new species not previously recorded in the region, from pelagic fish to sedentary invertebrates (Pitt et al. 2010, Last et al. 2011, Robinson et al. 2015). One such species suspected of undergoing a range shift into the area is the eastern rock lobster, *Sagmariasus verreauxi* (H. Milne Edwards, 1851). Eastern rock lobster is a large species of spiny lobster found along the east coast of Australia between southern Queensland and northern Tasmania, as well as off New Zealand. There is evidence that *S. verreauxi* is becoming more common further south along the Tasmanian east coast (Robinson et al. 2015), although isolated individuals have been reported over many decades. This potential range shift has implications for both fisheries and ecological management. While not currently a targeted fisheries species in Tasmania due to low abundance, continued ocean warming and increased *S. verreauxi* recruitment may facilitate a new lobster fishery or compete with the more valuable existing southern rock lobster fishery (*Jasus edwardsii*) in the region.

Spiny lobsters have among the longest and most complex larval life cycles of any marine invertebrate, lasting for up to two years in some species, with these stages being important for dispersal and possible range extension (Phillips et al. 2006). These early life stages may also be more susceptible to effects of climate change and ocean warming than their juvenile and adult counterparts (Pörtner & Farrell 2008, Storch et al. 2011, Fitzgibbon et al. 2014b). The puerulus stage of the spiny lobster life cycle is a critical transitional stage from pelagic larvae to recruitment into the juvenile population. It is a nektonic, non-feeding stage that actively swims to settle onto suitable habitat substrate in coastal regions (Fitzgibbon et al. 2014a). Like many larvae settling into new communities, puerulus must survive the 'wall of mouths' in their new environment (Emery 1973, Hamner et al. 1988). Physiological performance, such as

escape speed is critical for survival for puerulus stage *S. verreauxi* and changes to escape speed with warming may have far-reaching effects for the local and potentially range-shifting population.

To understand the future capacity for potential range shifts, multiple measures of *S. verreauxi* thermal performance are investigated, specifically measures of aerobic metabolism and escape performance. The specific aim was to develop thermal performance curves for both measures of performance and determine if thermal optimums for each measure were similar or different. The hypotheses are firstly, that the measures of aerobic scope and escape speed will have different thermal optimums, based on previous work on *S. verreauxi* juveniles that showed differences in other measures of performance (Fitzgibbon et al. 2017). And secondly, that escape speed will not change with temperature as it is an important survival trait and is likely strongly selected for and will hence be less effected by environmental changes.

Methods

Animal collection and holding

Puerulus stage eastern rock lobster, *Sagmariasus verreauxi*, were reared from eggs at the Institute for Marine and Antarctic Studies (IMAS) aquaculture facility in Hobart, Australia, as described by Fitzgibbon and Battaglene (2012) and Fitzgibbon et al. (2012). Fertilised eggs from different brood stock individuals were reared together, resulting in a mixed pool of larvae from which individuals for experimental trials were haphazardly selected. After metamorphosis from phyllosoma to puerulus stage larvae, animals were transferred to individual cylindrical vessels (300 mL) suspended in a 68 L polypropylene sump. Each sump held nine vessels, each with a single puerulus within, with each temperature treatment conducted in a separate sump. Each vessel had a 5 mm oyster mesh shelter for the pueruli, a

mesh bottom and received water circulated from the sump. The sumps were supplied with flow-through filtered seawater from a larger temperature-controlled sump at a rate of 50 L h-1 (0.74 exchanges per hour). An air stone was used to increase mixing and aeration within each sump, which was maintained above 100% dissolved oxygen saturation. Upon placement of pueruli into this holding system, they were held for a period of 7-9 days at 21°C before any experimental treatments were applied. This was done to eliminate any effects of the moulting cycle on the metabolic measurements but was limited by the time period before subsequent moults. *Sagmariasus verreauxi* are pueruli for approximately 21 days, and trials were conducted from age 10-15 days, making sure that there was no effect of moulting on the trials (Fitzgibbon et al. 2014a). Animal holding was conducted under a 12h light:12h dark regime and marine seawater (33-35 parts per thousand) salinity conditions.

Experimental procedure

Pueruli were assessed for metabolic rates and escape speed at six different temperature treatments; 20, 22, 24, 26, 28 and 30°C (n = 6, 6, 6, 10, 10 and 9 replicates, respectively; 0.131 ± 0.052 g wet weight). This temperature range spanned thermal regimes experienced by *S. verreauxi* as well as those above that may be reached with future ocean warming. From the holding temperature of 21°C, each of the six temperature treatments were reached by increasing or decreasing the temperature via submersible heaters (Carel ir33, www.carel.com) by 2°C per day followed by a two-day acclimation period. Temperatures remained stable within ±1°C of the set temperature. Due to different times taken to reach trial temperatures, between 20 and 30°C there is an age difference in the puerulus of five days. Even with the age differences, all puerulus remained within the stable intermoult period for the species and life stage (Fitzgibbon et al. 2014a).

Metabolic rates measured at each of these temperatures included standard metabolic rate, routine metabolic rate, and active metabolic rate, with aerobic scope calculated (aerobic scope

= active metabolic rate – standard metabolic rate) (e.g. Fitzgibbon et al. 2014b). Excess post-exercise oxygen consumption (EPOC) and recovery time were also measured for each individual (Gaesser & Brooks 1984). For the escape speed trials, maximum (burst) speed, average speed and number of escape responses were measured. Both metabolic and escape speed trials were run concurrently. Pueruli were first placed into the intermittent flow respirometry chambers for 16 hours to calculate standard and resting metabolic rates. After this period, they were placed into the escape speed arena and manually chased by hand for an approximately 9 min period while being video recorded for later analysis of escape speed, before being replaced into the respirometry chambers to measure active metabolic rates, EPOC and recovery time measurements for a further 24 hours. To clarify, for each puerulus, metabolic rate, escape speed and recovery data measurements were gathered.

Respirometry

Oxygen consumption rates of *S. verreauxi* pueruli were measured using an intermittent flow respirometry system as described by Fitzgibbon et al. (2014b). The system comprised four 19 mL glass micro-respiration chambers (Loligo horizontal mini chambers, www.loligosystems.com) connected to four twin channel mini peristaltic pumps (Harvard Apparatus Mini-Peristaltic Pump II, www.harvardapparatus.com). Two pumps ensured circulation within the chambers and past the dissolved oxygen sensor at all times, and two pumps provided the open-close flushing of the chambers that replenished the oxygen levels to ambient conditions in the respirometry chambers. The chambers were submerged in a 3.5 L outer tank maintained at the trial temperature by a sump with a submersible heater supplied with flow-through filtered seawater. The chambers were connected to oxygen sensors that measured dissolved oxygen levels every 20 s (PreSens OXY-4 Mini multichannel fibre optic oxygen transmitter, www.presens.de). The system was set to a 10 min on, 10 min off cycle allowing for three metabolic oxygen consumption measurements per hour.

Pueruli were placed in their respective chambers in the afternoon and left undisturbed for a period of 16 h. The first two hours of the oxygen consumption data were discarded to allow for chamber acclimation by the pueruli, and the following 14 h of data used to calculate the standard metabolic rate, using the average of the five lowest oxygen consumption values, and resting metabolic rate, calculated as the average of all measures in the 14 h period. After this 16 h period, the pueruli were removed individually from their chamber at the beginning of an open cycle and placed into a 100 L (59 cm diameter) round chase arena. The pueruli were chased for a nine min period to simulate exercise to exhaustion (see below for more details on concurrently run escape speed trials). This was done sequentially, with one puerulus chased at a time. The exercised individual was then returned to its original respirometry chamber and left for a further 24 h. This period was used to calculate the active metabolic rate (average of the two highest oxygen consumption values), as well as EPOC and time taken to recover to resting metabolic rate. Time taken to recover was estimated when the individual's metabolic rate came back to within two standard deviations of pre-exercise resting metabolic rate. Excess post-exercise oxygen consumption was calculated by the area under the curve. All respirometry trials were conducted under a 24h light regime to minimise activity to allow for accurate standard metabolic rates to be recorded.

After respirometry trials were completed, pueruli were removed from their chambers and wet mass weighed. Background respiration was measured simultaneously for each trial via one of the four chambers being left empty and subject to the same conditions and sampling intervals as those with trial pueruli.

Escape speed trials

Escape speed trials were recorded using a stereo video setup with twin GoPro video cameras (GoPro HERO4, www.gopro.com). A stereo video system allows for highly accurate measures of distance and speed in three-dimensions to be made, irrespective of the direction of the escape

response (Harvey et al. 2002). Twin GoPro cameras were housed in waterproof SeaGIS housings (SeaGIS custom housings, www.seagis.com.au) mounted on a stainless-steel frame with the cameras angled inwards 15 degrees from the perpendicular to allow sufficient overlap of both of the camera's fields of view. The cameras were programmed to a high-speed capture rate of 120 frames per second (fps) with a resolution of 720p (1280x720 pixels). The high frame rate allowed for accurate body velocity measurements to be calculated. The camera set-up was mounted above the 100 L, 59cm diameter round chase arena supplied with filtered seawater at the same temperature as used in the respirometry trial. The tank was equipped with an air stone for circulation and an external light source to provide sufficient light for filming. Upon completion of the first 16 h of respirometry trials, pueruli were removed from their chamber and placed in the chase arena. Here, they were manually chased for a period of approximately nine minutes (deemed long enough for the puerulus to reach exhaustion, as well as to coincide with the flushing period of the respirometry trials). This manual chasing included gently tugging with hands on the antennae and legs and gently prodding the body to illicit an escape response. The pueruli were stimulated continually during this period. Escape responses were defined as events when the pueruli responded with a tail flick response to 'escape' the stimulus. After this period, the puerulus was removed from the arena and placed immediately into its original chamber to continue the respirometry trial. Several measures of performance were taken for escape speed for the entire nine-minute trial duration; (i) the maximum speed reached by each puerulus (simulated single escape response), (ii) the average escape speed (average of all escape speeds measured during the nine-minute interval, simulating performance of individuals undertaking multiple escape responses) and (iii) the total number of escape responses exhibited by each pueruli.

Data and statistical analysis

All data and statistical analyses were performed using MS Excel®, EventMeasure Stereo (SeaGIS software, www.seagis.com.au) and the R statistical program (R Core Team 2017). Oxygen consumption rates were calculated in Excel where linear regressions were applied to raw oxygen concentrations to determine the decrease in oxygen concentration over the closed chamber period (nine minutes) before being transformed to an hourly consumption rate (h). These consumption values were corrected for background respiration and puerulus dry mass (DW), with final metabolic rates expressed as mg O2 gDW^{-1} h^{-1}. Oxygen consumption rates were ascertained using dry weight, estimated as 22% of the wet weight measured, based on data from Fitzgibbon et al. (2014a). Background respiration was measured simultaneously as trials were conducted and was accounted for by subtracting background oxygen consumption values from the oxygen consumption values of the pueruli measurements. Recovery measures were calculated as the time and magnitude taken for metabolic rates to come back within two standard deviations of resting metabolic rates. Magnitude of EPOC was the sum of the area under the curve between measured metabolic rates after exercise minus the resting metabolic rate plus two standard deviations. The stereo video footage was analysed using EventMeasure Stereo with distance travelled calculated in three dimensions (X, Y, Z coordinates) while the frame rate gave the time taken to complete the escape response. Velocity (in metres per second) was then calculated using the following adapted Pythagoras equation:

$$\boldsymbol{Velocity} = (\frac{\sqrt{(\boldsymbol{X_{end}} - \boldsymbol{X_{start}})^2 + (\boldsymbol{Y_{end}} - \boldsymbol{Y_{start}})^2 + (\boldsymbol{Z_{end}} - \boldsymbol{Z_{start}})^2}}{\boldsymbol{Number\ of\ video\ frames}}$$

Where X, Y and Z are the three-dimension coordinates and are separated into ‘start’ position and ‘end’ position of the escape response, and the number of video frames taken to complete the responses from start to end frame.

Regression modelling was used analyse relationships between measured variables and temperature. Metabolic rates, EPOC and escape responses (maximum and average speeds as well as number of escape responses) were assessed for normality using residual plots and analysed using linear and linear mixed models. Recovery time was analysed using a binomial response model. Model selection used Akaike's Information Criterion (AIC) to determine the best fit model. Where appropriate, optimal temperatures (Topt) for the thermal performance curves were calculated using the first derivative of the quadratic equation from the regression analysis. Pearson's correlation tests were used to identify parameters that were significantly correlated.

Results

Metabolic rates, EPOC and escape response parameters were examined with linear, and linear mixed models, however in all instances the simple linear models fit better than the linear mixed models as determined by AIC values. Therefore, all regression models referred to herein are linear models.

Pueruli metabolic rates all increased significantly with temperature, with different regression exponents (Figure 2.1). Regression analyses showed routine and active metabolic rates increased exponentially with temperature, while standard metabolic rate increased linearly (Figure 2.1a, Table 2.1). Aerobic scope was best described by a quadratic regression where the measure peaked at ~27°C (Figure 2.1b, Table 2.1). Mortality only occurred at the higher temperatures, with one, one and three mortalities in the 26, 28 and 30°C treatments, respectively. These mortalities occurred during the respirometry phase after the animals were exercised. The measurements of the animals that died during the trials were excluded from all regression analyses.

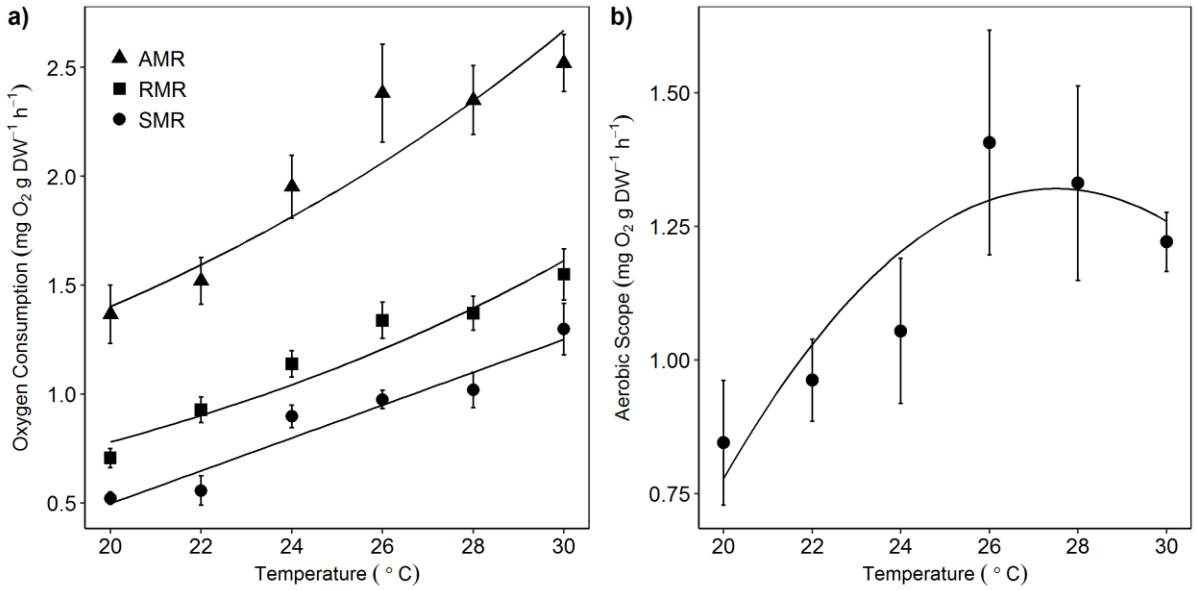

Figure 2.1. Effect of temperature on aerobic metabolism of *Sagmariasus verreauxi* pueruli, including a) active metabolic rate (AMR), routine metabolic rate (RMR), standard metabolic rate (SMR), and b) aerobic scope. Values are mean ± 1 SE. Sample size ranged from 6 to 10 individuals per temperature treatment. Details for regressions are provided in Table 2.1.

Recovery rates, time and EPOC, showed different responses to temperature (Figure 2.2). At all temperatures, many individuals were able to recover quickly. However, at temperatures 26°C and above, some individuals showed large increases in both recovery time and EPOC. For recovery time, there was a clear division between individuals that recovered quickly and those that did not (Figure 2.2a). A binomial response model showed temperature affected whether not an individual came back to its resting metabolic rate quickly or not, with predicted recovery decreasing with increasing temperature (Wald test $\chi^2 = 6.7$, $p = 0.010$). Individuals that took longer to recover had associated larger values of EPOC. However, exponential regression analysis showed there was no significant effect of temperature on EPOC measurements ($F(1,44) = 0.617$, $p = 0.436$, Figure 2.2b).

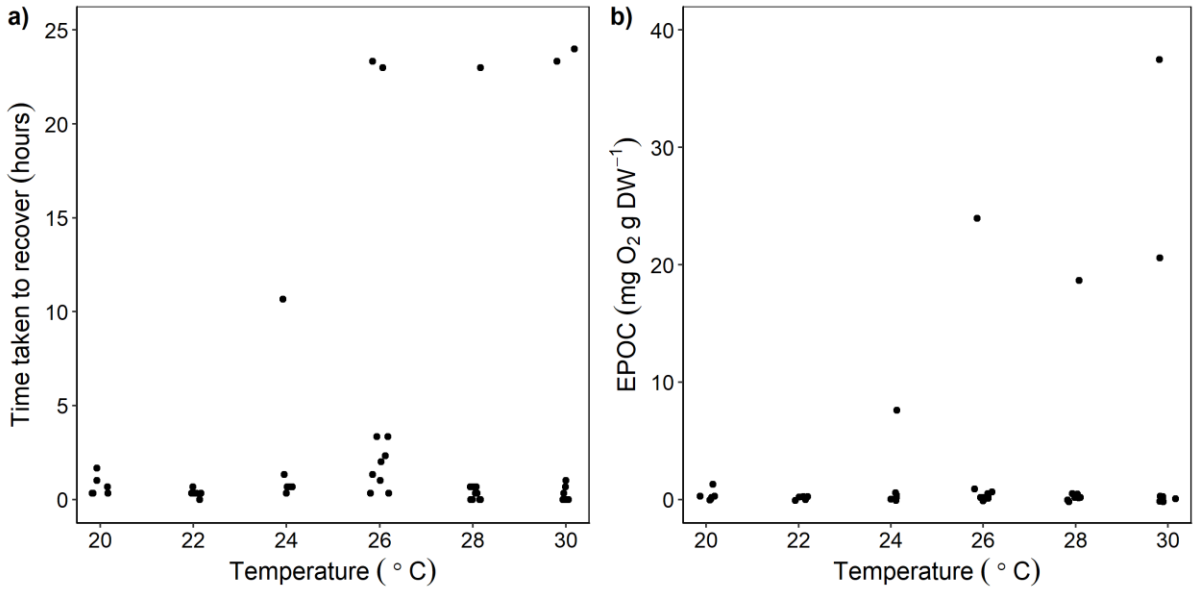

Figure 2.2. Recovery measurements of *Sagmariasus verreauxi* pueruli including a) recovery time data and b) excess post-exercise oxygen consumption (EPOC). Sample size ranged from 6 to 10 individuals per temperature treatment. Details for EPOC regression are provided in Table 2.1.

Analysis of two measures of escape speed, maximum escape (single burst response) speed and average escape speed (average of all escape responses) showed both responses were non-significant across the temperature range tested ($F(2,42) = 3.153$, $p = 0.053$ and $F(2,42) = 3.158$, $p = 0.053$ respectively, Figure 2.3a, Table 2.1). The number of escape responses did not differ significantly with temperature (Figure 2.3b, Table 2.1).

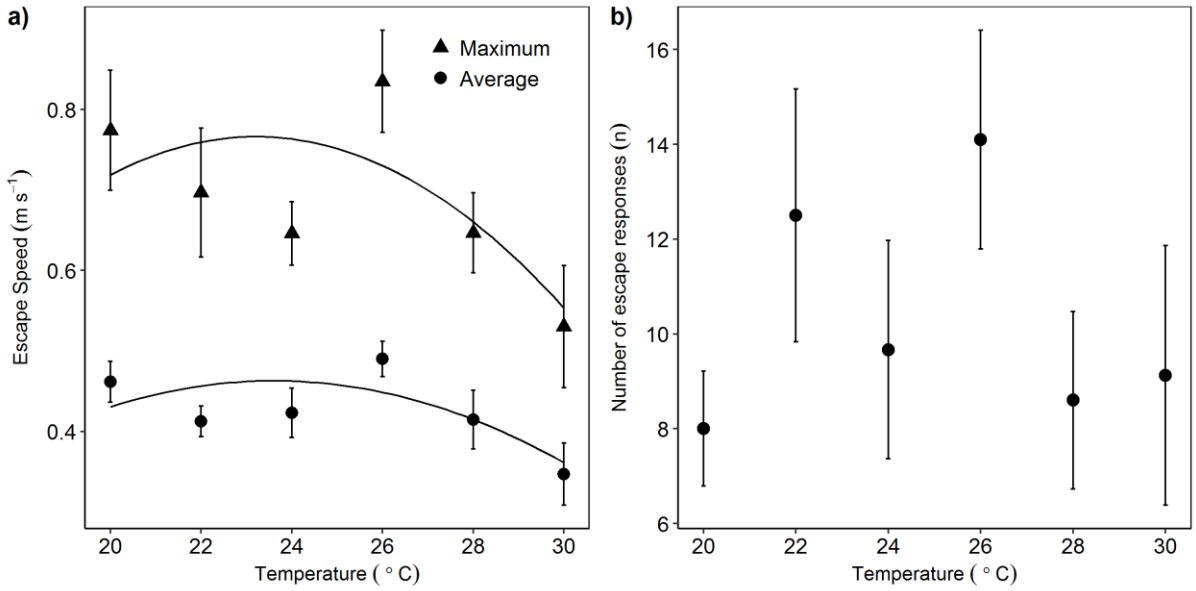

Figure 2.3. a) Maximum and average escape speeds, and b) number of escape responses exhibited by *Sagmariasus verreauxi* pueruli. Values are mean ± 1 SE. Sample size ranged from 6 to 10 individuals per temperature treatment. Details for regressions are provided in Table 2.1.

Table 2.1. Results of regression analyses of different performance responses to temperature of *Sagmariasus verreauxi* pueruli. Abbreviated measures are active metabolic rate (AMR), routine metabolic rate (RMR), standard metabolic rate (SMR) and excess post-exercise oxygen consumption (EPOC). Analyses in the form of linear ($y = ax + b$), exponential ($y = e^{a + bx}$) and quadratic ($y = ax^2 + bx + c$) regressions. * indicates significance at $p < 0.05$.

	Regression	a	b	c	R^2	df	F	p
AMR	Exponential	0.065	-0.952	-	0.4845	44	41.35	0.007*
RMR	Exponential	0.073	-1.700	-	0.6325	44	75.72	<0.001*
SMR	Linear	0.075	-1.010	-	0.5863	44	62.36	<0.001*
Aerobic Scope	Quadratic	-0.010	0.531	-5.983	0.1481	43	3.738	0.032*
EPOC	Exponential	0.5415	-0.106	-	0.0138	44	0.617	0.436
Maximum Speed	Quadratic	-0.005	0.214	-1.720	0.1306	42	3.154	0.053
Average Speed	Quadratic	-0.002	0.118	-0.926	0.1307	42	3.158	0.053
Number of escape responses	Quadratic	-0.149	7.411	-80.008	0.0531	43	1.206	0.309

Results of Pearson correlation tests showed a significant positive relationship between log-transformed recovery time and log-transformed magnitude of EPOC values ($r(44) = 0.943$, $p < 0.001$). There was a weak correlation between aerobic scope and log-linear EPOC values ($r(44) = 0.325$, $p = 0.027$) but not between aerobic scope and log-linear recovery times ($r(44) = 0.281$, $p = 0.058$). There was no significant correlations between aerobic scope and maximum escape speed ($r(43) = -0.116$, $p = 0.448$) or between maximum escape speed and log-linear recovery measures (recovery time $r(43) = -0.007$, $p = 0.961$; EPOC $r(43) = 0.005$, $p = 0.976$). There was a significant positive correlation between average escape speed and puerulus weight ($r(43) = 0.326$, $p = 0.029$), but not between maximum escape speed and weight ($r(43) = 0.281$, $p = 0.061$). Level of activity (i.e. number of escape responses, Figure 2.3b), did not correlate with longer recovery times or the magnitude of EPOC ($r(44) = 0.191$, $p = 0.203$ and $r(44) = 0.1664$, $p = 0.276$, respectively).

Discussion

Sagmariasus verreauxi pueruli exhibit different thermal optimums for multiple measures of species performance. The optimal temperature results for aerobic scope and escape speed support increasing evidence that suggests that a single measure of performance, namely aerobic scope, may not accurately predict whole animal performance under ocean warming scenarios (Clark et al. 2013, Norin et al. 2014, Fitzgibbon et al. 2017).

Differences in thermal tolerances between performance measures

Different thermal optima of different measures of performance have been found in a range of marine species, as well as across different life stages in the same species. In juvenile *S. verreauxi*, optimal growth temperatures did not match the thermal optimum for aerobic scope (Fitzgibbon et al. 2017). This has also been reported in other species, such as barramundi (*Lates*

calcarifer), where different thermal optimums were found for juvenile feed intake and growth performance (Katersky & Carter 2007) and aerobic scope was also not found to be a predictor of behavioural thermoregulation or performance for juveniles of the same species (Norin et al. 2014). The optimal temperature for escape speed (while it did not significantly change with temperature) was lower than those for aerobic scope, indicating that while an individual may have the aerobic capacity to survive and perform well in some areas, escape speed could potentially be a limiting factor in whole organism performance at higher temperatures, potentially resulting in mortality due to being unable to escape a predator. Collectively, this shows multiple performance measures can have different thermal optimums which may contribute differently to how a species copes with ocean warming.

Measures of performance may also have differing thermal optimums at different life stages. Prior studies have suggested that larval stages of marine species may be more susceptible to climate change (Pörtner & Farrell 2008). While there have been studies on aerobic scope in juvenile stages of *S. verreauxi* (Fitzgibbon et al. 2017), we are not able to draw conclusions on whether the puerulus stage may be more vulnerable than the juvenile stage due to differences in the methods of the studies and the results. To elaborate, maximum temperatures tested differed (25°C compared to 30°C in this study), acclimation times differed (60 days compared to two days in this study) and the results showed different thermal patterns (exponential increase in aerobic scope to 25°C in juveniles, compared to a peak in optimal performance at 27°C in this study). As there is no comparable study on the thermal tolerance of escape speed of other life stages of this species, we cannot yet judge if this pattern holds true either.

Escape speed as an important survival factor

Escape speed is considered to be an important survival factor in predation interactions and therefore escape speed performance may be a highly selected trait (Dell et al. 2011). Model results found that the effect of temperature on both maximum and average escape speed was

not significant ($p = 0.053$ and $p = 0.053$ respectively, Figure 2.3a, Table 2.1), which suggests that speed may be relatively unaffected by changes in temperatures. This may be due to escape speed being a critical survival measure for a prey species to be able to survival a predator attack (Dell et al. 2011). Other studies investigating the effect of temperature on escape responses have shown mixed results, with some finding that the temperatures they tested did not affect escape speed (Killen et al. 2015), while others found that temperature had a significant effect on escape speed (Johnson & Bennett 1995). The difference between escape speed performance suggests that the mechanisms driving how organisms escape from predators varies between species and may be influenced by changing ecosystem pressures throughout different life stages. As escape speed in *S. verreauxi* appears to be unaffected by temperature, it suggests that escape speed during this life stage may be important for survival and is therefore strongly selected for. However, as predator attack speeds are also likely to alter with warming, predicting the outcome of predator-prey interactions may be complicated (Dell et al. 2011).

Recovery measures

Recovery time and EPOC showed different patterns of response to temperature. For time taken to recover to pre-exercise routine metabolic rate, there was a separation between animals at the higher temperatures that recovered relatively quickly, and those that did not come back to their routine metabolic rate for the remaining duration of the experiment. This separation may indicate that some individuals in the population, those able to recover quickly, may have sufficient phenotypic plasticity to survive and a potentially increased capacity to adapt to future temperatures (Foo & Byrne 2016). The longer recovery times were correlated with higher values of EPOC. Longer recovery times have also been associated with higher temperatures in other marine invertebrates (Schalkhausser et al. 2014), as well as with individuals that are more vigilant (Killen et al. 2015). These results indicate that there may be higher costs associated with higher temperatures, such as longer recovery times which may in turn affect survival. At

26, 28 and 30°C, this cost resulted in death during respirometry trials for some pueruli (n=1, 1 and 3, respectively). As the puerulus stage is a non-feeding stage in the life cycle (Phillips et al. 2006), the energy available to them is limited until they moult into their juvenile feeding stage. Thus, this stage is considered to be a potential bottleneck for the population in terms of recruitment success due to high energy demands associated with near-shore settlement while having a fixed energy supply (Fitzgibbon et al. 2014a). Higher future temperatures coupled with predation pressure may have serious consequences for individuals as they may not be able to recover sufficiently to transition to their next life stage.

Ecological implications and potential future changes

The extension of the East Australian Current in the region (Ridgway 2007) has already facilitated the range extensions of many other species into, and further south in Tasmania, including pelagic fish species favoured by fishers such as pink snapper, *Pagrus auratus* (Last et al. 2011) and species that have been detrimental to coastal environments such as the long-spine sea urchin, *Centrostephanus rodgersii* (Ling et al. 2009, Johnson et al. 2011). This warming and increase in transport will likely facilitate increased arrival and survival of *S. verreauxi* pueruli in Tasmanian waters in future years with ocean warming. In addition to a possible range extension at the polewards range edge of their distribution, it is also likely that *S. verreauxi* will undergo a range contraction at their equatorward range edge (Fitzgibbon et al. 2014b). As temperatures in the equatorward edge of their range currently reach 28°C (Montgomery et al. 2009), with future ocean warming it is likely that ambient temperature will exceed those that are optimal, leading to decreases in performance of puerulus and hence a likely decrease in settlement and survival, resulting in a range contraction at the warmer range edge for the species.

Conclusion

The variability in the investigated measures of performance has implications for the species in terms of selection of particular phenotypes (Clark et al. 2017), recruitment success (Fitzgibbon et al. 2014b) and interactions with other species (Dell et al. 2011). While this study considered multiple possible capacities affecting range shifts, future work should include other measures of performance, including growth at different life stages, reproductive capacity, as well as other measures of species interaction success such as competitive ability for resources and performance of predators. It would also be valuable to identify potential life history bottlenecks that may have a disproportionate effect on populations and examine the thermal tolerances of these particular stages. The more performance measures that are investigated, the greater confidence we will have regarding our capacity to predict responses to future change. In addition, investigating the thermal tolerances at the cooler edge of the species range would be valuable in determining the implications for settlement survival and species success in the cooler waters of Tasmania. Measures of species performance, including those representative of species interactions, will help develop mechanistic models and more robust and accurate future predictions (Evans et al. 2015).

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CHAPTER 3

Mismatch of thermal optima between performance measure, life stage and species of spiny lobster.

Abstract

Ocean warming is driving species' redistribution in marine environments globally. Understanding how ocean warming may affect species and their propensity to shift their distribution in response is important in managing our changing marine environment. In an ocean warming hotspot off south-east Australia, many species have expanded their ranges polewards including the eastern rock lobster, *Sagmariasus verreauxi*, which is currently thought to be extending its range via larval advection into Tasmanian regions occupied by the more commercially important southern rock lobster, *Jasus edwardsii*. Here, thermal tolerances of the two lobster species at two life stages are determined to investigate how temperature affects both species. The pattern, optimum and magnitude of thermal responses differed between performance measures, life stage and species. *Sagmariasus verreauxi* had a higher thermal tolerance for aerobic scope than *J. edwardsii*. However, while *S. verreauxi* had a higher optimal temperature for escape speed, *J. edwardsii* had a higher overall magnitude of escape speed, indicating a higher capacity for escape performance. This inconsistency in performance optima and magnitude indicates that a single performance measure at a single life stage is unlikely to accurately predict whole-animal performance. Species success and survival in response to environmental changes will depend on how specific ecosystem pressures affect performance traits most relevant to a particular life stage. Results suggest that with continued ocean warming, *S. verreauxi* is likely to continue to expand in distribution and increase in abundance in Tasmania, with implications for interactions between the two lobster species and for the local ecosystem.

Keywords: *aerobic scope, climate change, crustaceans, escape speed,* Jasus edwardsii, *range shift,* Sagmariasus verreauxi.

Introduction

Climate change is causing widespread alterations to species' geographical ranges in marine communities worldwide (Parmesan & Yohe 2003, Pitt et al. 2010, Last et al. 2011, Pinsky et al. 2013, Poloczanska et al. 2013, Pecl et al. 2017). As ocean temperatures rise, many marine species have been observed extending their range boundaries in a generally polewards direction (Sunday et al. 2012, Poloczanska et al. 2013). However, the pace at which species change their distribution occurs at different velocities, likely changing their interaction with other species, with ramifications for food webs and potentially widespread modifications of ecosystems (Ling 2008, Johnson et al. 2011, McLeod et al. 2012, Sunday et al. 2015). Understanding if and how species may shift their range under warming scenarios and how species interactions may change, is critical to understanding the complex effects of climate change on marine ecosystems.

Thermal performance curves have been a common approach to assess species responses to temperature and more recently to climate warming (Fry 1947, Angilletta 2009, Sinclair et al. 2016). They map changes of a particular performance measure (e.g. metabolism, growth) against changes in temperature to derive a species' optimal or suboptimal temperatures (Pörtner & Knust 2007, Pörtner & Farrell 2008, Schulte et al. 2011, Sinclair et al. 2016). This approach is particularly useful for ectothermic organisms whose body temperature and associated body functions are directly affected by ambient temperature (Pörtner & Farrell 2008, Angilletta 2009). These measures of performance can be any temperature-dependent biological rate such as metabolism, growth, reproduction and escape speed (Donelson et al. 2014, Fitzgibbon et al. 2017, Twiname et al. in review). Ecologically-relevant thermal performance information has the potential to inform and help predict possible changes in organism performance in a changing climate and facilitate predictions of future range shifts (Evans et al. 2015).

While thermal performance curves are used to predict thermal sensitivity in a single species, they may also be a useful tool to predict the potential changes in outcomes of species interactions. Species range shifts can alter species interactions, such as predator-prey relationships or competitive interactions for resources, in multiple ways (Kordas et al. 2011, Dell et al. 2014, Lord et al. 2017). One of these is the development of novel species interactions due to asynchronous distribution shifts, where some organisms extend their ranges to new areas, creating new interactions with the resident species (Johnson et al. 2011, Marshak & Heck 2017). Another is the modification of existing interactions, through changes in the abundance of species, or changes in relative performance of one or both species (Milazzo et al. 2013). It is unlikely that both species in an interaction will react to changes in temperature the same way and hence asymmetries will arise in the response and outcomes of interactions (Grigaltchik et al. 2012, Dell et al. 2014). Depending on their individual thermal physiologies, a measure of performance may increase or decrease depending on their thermal optimum and their current thermal habitat. For example, at the warm edge of a species range, further warming may reduce performance of measures such as swimming performance (Johansen & Jones 2011). In contrast at the cool end of their range, warming may increase swimming performance (Batty & Blaxter 1992, Temple & Johnston 1998). Using thermal performance curves will help identify how individual species react to changes in ocean temperatures and inform at what temperature outcomes of species interactions will change.

One common measure of physiological performance used to investigate effects of temperature is aerobic scope (Fry & Hart 1948, Pörtner & Knust 2007, Clark et al. 2013). Aerobic scope is the difference between maximum and resting oxygen consumption rates (Fry & Hart 1948) and estimates the amount of aerobic energy available – in excess of that consumed by basic body functions – to support other essential activities such as feeding. The use of aerobic scope measurements to predict whole organism performance changes under ocean warming has been

widely implemented and discussed, with support for and against its use (Pörtner & Knust 2007, Clark et al. 2013, Pörtner et al. 2017, Jutfelt et al. 2018). The oxygen and capacity-limited thermal tolerance hypothesis proposes aerobic scope as a unifying proxy for animal fitness and suggests that species select temperatures to maximise aerobic scope (Pörtner & Knust 2007). However, there is increasing evidence from recent studies indicating that aerobic scope may not be sufficient to predict whole animal performance and that the oxygen and capacity-limited thermal tolerance hypothesis lacks the capacity to be used as a unifying proxy (Norin et al. 2014, Verberk et al. 2016, Fitzgibbon et al. 2017, Jutfelt et al. 2018, Twiname et al. in review).

Escape speed presents another ecologically relevant performance measure that changes with temperature and is critical to survival often within a matter of seconds (Batty & Blaxter 1992, Domenici & Blake 1997, Dell et al. 2011). If a species' escape speed changes with ocean warming, outcomes between predator and prey may change, which may cause major shifts in the structure and function of an ecosystem (Grigaltchik et al. 2012, Dell et al. 2014, Ohlund et al. 2015). In contrast to aerobic scope, escape bursts are mostly powered anaerobically by white muscle and linked to aerobic metabolism only during recovery (Ellington 1983, England & Baldwin 1983, De Zwaan & v.d. Thillart 1985). For most species it is unknown whether optimal temperatures for two critical but independent performance measures – aerobic scope and escape speed – align or mismatch. Further, the use of multiple ecologically relevant thermal performance curves can improve our understanding of how species performance may alter with changes in their thermal environment under ocean warming and provide the knowledge to increase the adaptive and management capacity for marine resources.

In south-east Australia, range shifts are bringing species into areas they have rarely been recorded previously (Ling 2008, Pitt et al. 2010, Last et al. 2011, Robinson et al. 2015). One of these species is the eastern rock lobster, *Sagmariasus verreauxi*, commonly found along the south-east coast of mainland Australia and sporadically in northern Tasmania (Montgomery &

Craig 2005). However, with recent warming, this species is considered likely to be undergoing a range-shift further into Tasmanian waters (Robinson et al. 2015). This potential expansion is likely facilitated by the increase in the strength and extent of the East Australian Current in south-east Australia, bringing more sub-tropical larvae further poleward (Booth et al. 2007, Ridgway 2007, Figueira et al. 2009, Ling et al. 2009, Cetina-Heredia et al. 2015). This range-shifting species is thought to be moving into areas dominated by the local species, the southern rock lobster, *Jasus edwardsii*, with novel interactions between the species, either through new interactions or changes in abundance of the interacting species. Both species are ecologically-important species and have significant economic and social value for fisheries in south-east Australia (Montgomery & Craig 2005, Montgomery et al. 2009, Pecl et al. 2009). It is uncertain how increasing temperatures and a novel biotic interaction between range-shifting *S. verreauxi* and the more commercially valuable *J. edwardsii* will change their important ecological and economic roles. Understanding their sensitivity to ocean warming and how this will affect outcomes of their mutual interaction is critical to apply supportive and sustainable management practice for both species.

To address the potential (mis)match in optima between thermal performance measures, a widely applied physiological performance indicator, aerobic scope, was compared with an independent ecologically important performance indicator, escape speed, at a larval (puerulus) and juvenile life stage of *J. edwardsii* and *S. verreauxi*. This study expands on previous work investigating one species and life stage of *S. verreauxi* (Twiname et al. in review), where a new species and life stage allow for life history and interspecific comparisons to be made. The hypotheses that (i) due to their thermal histories, *S. verreauxi* will have higher thermal optima for the measured performance traits than *J. edwardsii*, (ii) the species' will have different thermal optima for two independent performance measures and (iii) there will be cross over

temperatures where the thermal performance curves of both species overlap, highlighting potential gradients in interaction outcomes, were tested.

Methods

Animal collection and holding

Sagmariasus verreauxi puerulus (n = 51, wet weight (mean ± one standard deviation) 0.31 ± 0.05 g) were cultured from eggs at the Institute for Marine and Antarctic Studies (IMAS) by procedures similar to those described by Fitzgibbon et al. (2012) and held prior to experimentation as per Twiname et al. (in review). *Jasus edwardsii* puerulus (n = 29, wet weight 0.43 ± 0.08 g) were collected monthly from puerulus collectors located at Bicheno (41.85° S, 148.26° E), Iron Pot (43.06° S, 147.42° E) and Recherche Bay (43.55° S, 146.90° E), along the eastern and southern coasts of Tasmania. Pueruli collected were transported back to IMAS and placed into 65 L holding tanks supplied with the same filtered seawater as for *S. verreauxi* pueruli. Juvenile *S. verreauxi* (n = 24, wet weight 47.88 ± 12.97 g, carapace length 48.68 ± 4.82 mm) were also cultured from eggs at IMAS, and *J. edwardsii* juveniles (n = 36, wet weight 37.22 ± 7.45 g, carapace length 42.77 ± 3.16 mm) were selected from a stock of individuals collected in previous years as pueruli and reared at the IMAS facilities. All individuals were held species separated for the entire trial. Individuals of both species were selected for trials based on size and time since moulting. As *S. verreauxi* grow faster than *J. edwardsii*, individuals selected for the trials were of similar size but were different ages (i.e. one-year old *S. verreauxi* compared to two-year old *J. edwardsii*). Juvenile lobsters of each species were held separately in 5000 L tanks supplied with unfiltered sea water until they moulted, after which experiments began. Juvenile lobsters were fed 2-3 times per week to excess with fresh or thawed blue mussels (*Mytilus galloprovincialis*). Once a lobster of either species moulted, they were transferred into 65 L holding tanks at ambient temperatures for one

week prior to adjustment and acclimation to trial temperatures to reduce effects of moulting on metabolic or behavioural results. The holding tanks were supplied with filtered seawater and the juvenile lobsters were fed to excess with fresh or thawed blue mussels.

Experimental procedure

Trial temperatures (maintained within ± 1°C) were achieved by increasing or decreasing the water temperature, via a submersible heater (Carel ir33, Italy), by 2°C per day until the trial temperature was achieved. The 2°C heating or cooling per day was within the daily temperature variance experienced by lobsters in natural environments (Stobart et al. 2016). Puerulus had a two-day acclimation period and juveniles a minimum of seven days acclimation to trial temperatures before any experiments commenced. Pueruli had a shorter acclimation period due to the shorter larval stage duration. For *S. verreauxi* and *J. edwardsii* pueruli and *J. edwardsii* juveniles, six temperatures were investigated over different thermal ranges (20-30°C, 16-26°C and 16-26°C, all at 2°C intervals, respectively). Due to constraints on the number of available suitably-sized *S. verreauxi* juveniles, only five temperatures were investigated (22-30°C by 2°C intervals). Additionally, due to the short puerulus intermoult period, only three *J. edwardsii* puerulus replicates were conducted at 26°C i.e. only three individuals did not moult during or immediately after respirometry and escape speed trials. Of these three, only one individual responded to stimuli for the escape speed trials and exhibited a response and so the 26°C treatment for *J. edwardsii* puerulus was excluded from the escape speed analyses. For each of these temperatures, both aerobic metabolism and escape speed trials were conducted concurrently. Active metabolic rate, resting metabolic rate and standard metabolic rate were measured and aerobic scope was calculated (aerobic scope = active metabolic rate – standard metabolic rate) for each species and life stage. Time take to recover and excess post-exercise oxygen consumption (EPOC) were also measured during the aerobic metabolism trials (Gaesser & Brooks 1984). Escape performance measures examined maximum escape speed

(burst speed), average escape speed and number of escape responses exhibited by each individual.

Respirometry

Intermittent flow respirometry was used to investigate thermal effects on aerobic metabolism. For the puerulus, intermittent flow respirometry protocols were similar to that described as by Fitzgibbon et al. (2014b). Briefly, pueruli were placed in 19 mL glass respirometry chambers (Loligo horizontal mini chambers, Denmark) submerged in a 3.5 L sump supplied with ozonated, temperature-controlled seawater. Peristaltic pumps (Harvard Apparatus Mini-Peristaltic Pump II, USA) provided continuous recirculation past the oxygen sensors as well as chamber flushing every 10 minutes. Dissolved oxygen measurements were taken every 10s using a fibre optic dissolved oxygen analyser (PreSens OXY-4 Mini multichannel fibre optic oxygen transmitter, Germany), and remained between 75-100% saturation for the duration of the trials. Puerulus trials were started at approximately 16:00 and ran overnight for a period of 16 hours. During this period, standard and routine metabolic rates were measured. At approximately 08:00 the next day, pueruli were removed individually and placed into a chase arena (see Figure 3.1). The pueruli were manually chased for a period of approximately 9 minutes (see below) before being placed back into their respective chambers for another 24 h, where active metabolic rate and recovery parameters were measured.

For the juveniles, a similar protocol was followed but using a larger system similar to that described by Jensen et al. (2013). A 500 L sump was supplied with filtered seawater and fitted with a submersible heater to maintain water temperature, as well as two air stones for water circulation and aeration. Four custom-made Perspex respirometry chambers were placed in the sump, each connected to two pumps, a flush pump and a recirculation pump, ensuring water was pumped continuously across the dissolved oxygen probe (Hach Intellical LDO101 Luminescent Dissolved Oxygen sensor, USA). Dissolved oxygen measurements were taken

every 30 seconds during a 5 min open: 5 min closed cycle. Two chamber sizes were used to ensure that the dissolved oxygen levels never dropped below 75% saturation. Therefore, a larger-sized chamber (1000 mL) was used for individuals >50 g wet weight and a smaller chamber (485 mL) for lobsters <50 g. Trials confirmed that there was no significant difference in resting metabolic rate measurements taken between the two different sized chambers (paired t-test, $t(91) = 1.66$, $p = 0.179$).

Metabolic rates were determined by protocols similar that that described by Fitzgibbon et al. (2014a). Resting metabolic rate was calculated during the first 16 hours of the trial, with the first two hours of experimental data excluded to account for chamber acclimation. Active metabolic rate was the mean of the two highest metabolic measurements, and standard metabolic rate the mean of the lowest five metabolic measurements during the trial. Time to recovery was taken as when the metabolic rate came back to within two standard deviations of resting metabolic rate after the exercise period. Excess post-exercise oxygen consumption was calculated using the area under the metabolic curve after exercise to when it returned to resting metabolic rate + two standard deviations.

Escape speed trials

The escape speed trials were filmed when the individuals were removed from their chamber and placed in a chase arena supplied with filtered seawater at the same temperature as the respirometry trial. The escape responses were filmed using stereo video cameras (GoPro HERO4, USA), mounted on a custom-made stainless-steel frame holding the cameras at 15 degrees inwards from the perpendicular to the bar, allowing for overlap of the two camera fields of view (see Figure 3.1). The escape response videos were filmed at 240 frames per second (fps) and 720p (1280 x 720 pixels) resolutions. The high frame rate was used to ensure escape speed was accurately recorded and the stereo system to ensure accuracy when the lobsters did not escape in the direction of the camera field of view (Harvey et al. 2002). The

lobsters were chased for a period of time before being placed into their original chambers to continue the post-exercise metabolic trials. Chasing involved gently tugging on the antennae of the lobsters or gently prodding the legs and bodies by hand. For the pueruli, the chase arena consisted of the camera system mounted above a 100 L, 59 cm diameter tank. The chase period was approximately 9 minutes. For more details on the puerulus escape speed trials, see Twiname et al. (in review). For the juvenile escape speed trials, the camera system was mounted above a 300 L, 150 cm diameter arena and the chase period was approximately 13 minutes. Escape responses were defined as events when the individuals responded with a tail flick response to 'escape' the stimulus. During both sets of experiments, the lobster individuals were stimulated continually through the full trials (9 or 13 minutes for pueruli or juveniles, respectively). Several measures of performance were taken for escape speed for the entire trial durations; (i) the maximum speed reached by each individual (simulated single escape response), (ii) the average escape speed (average of all escape speeds measured during the duration interval, simulating performance of individuals undertaking multiple escape responses) and (iii) the total number of escape responses exhibited by each individual.

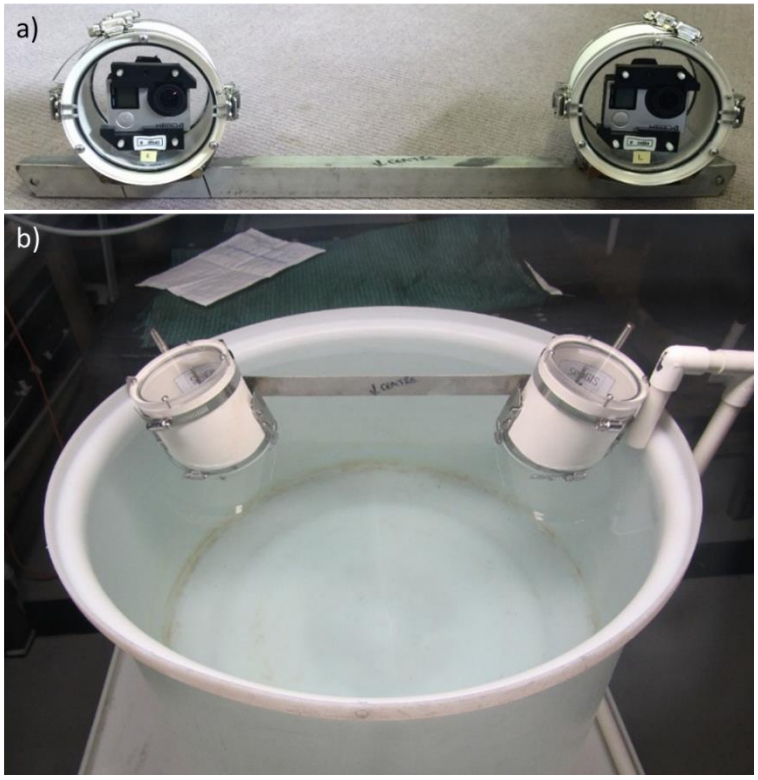

Figure 3.1. Stereo-camera set up used to film lobster escape responses. Two GoPro cameras fitted in waterproof housings on a stainless-steel bar (a) mounted above a well-lit chase arena (b).

Data and statistical analysis

Data and statistical analyses were performed using MS Excel®, EventMeasure Stereo (SeaGIS software, www.seagis.com.au) and the R statistical program (R Core Team 2017). Oxygen consumption rates were calculated in Excel and analysed using regression models in R. Oxygen consumption rates were calculated using whole-animal dry weight, estimated as 22% of the wet weight measured using an analytical balance (Fitzgibbon et al. 2014a). Background respiration was measured simultaneously during all trials and was accounted for by subtracting background oxygen consumption values from the oxygen consumption values of the trial measurements prior to correction for mass. Recovery measures were calculated as the time and magnitude taken for metabolic rates to come back within two standard deviations of resting metabolic rates. Magnitude of EPOC was the sum of the area under the curve between

measured metabolic rates after exercise minus the resting metabolic rate plus two standard deviations. The stereo video footage was analysed using EventMeasure Stereo with distance travelled calculated in three dimensions (X, Y, Z coordinates) while the frame rate gave the time taken to complete the escape response. Body velocity, or escape speed (in metres per second), was then calculated using Pythagoras's equation:

$$\boldsymbol{Velocity} = (\frac{\sqrt{(\boldsymbol{X_{end}} - \boldsymbol{X_{start}})^2 + (\boldsymbol{Y_{end}} - \boldsymbol{Y_{start}})^2 + (\boldsymbol{Z_{end}} - \boldsymbol{Z_{start}})^2}}{\boldsymbol{Number\ of\ video\ frames}}$$

Where X, Y and Z are the three-dimension coordinates and are separated into 'start' position and 'end' position of the escape response, and the number of video frames taken to complete the responses from start to end frame.

Regression modelling was used analyse relationships between measured variables and temperature. Metabolic rates, EPOC and escape responses (maximum and average speeds as well as number of escape responses) were assessed for normality using residual plots and analysed using linear and linear mixed models. A generalised linear model was used to assess the differences in performance measures between species and temperature. Model selection used Akaike's Information Criterion (AIC) to determine the best fit model. Where appropriate, optimal temperatures (Topt) for the thermal performance curves were calculated using the first derivative of the quadratic equation from the regression analysis. Pearson's correlation tests were used to identify parameters that were significantly correlated.

Results

All metabolic rates, except the active metabolic rate for *S. verreauxi* juveniles, increased significantly with temperature across their tested thermal range (Figure 3.2, Table S3.1). Model

relationships varied between species and life stage from linear to polynomial regressions (Figure 3.2, Table S3.1).

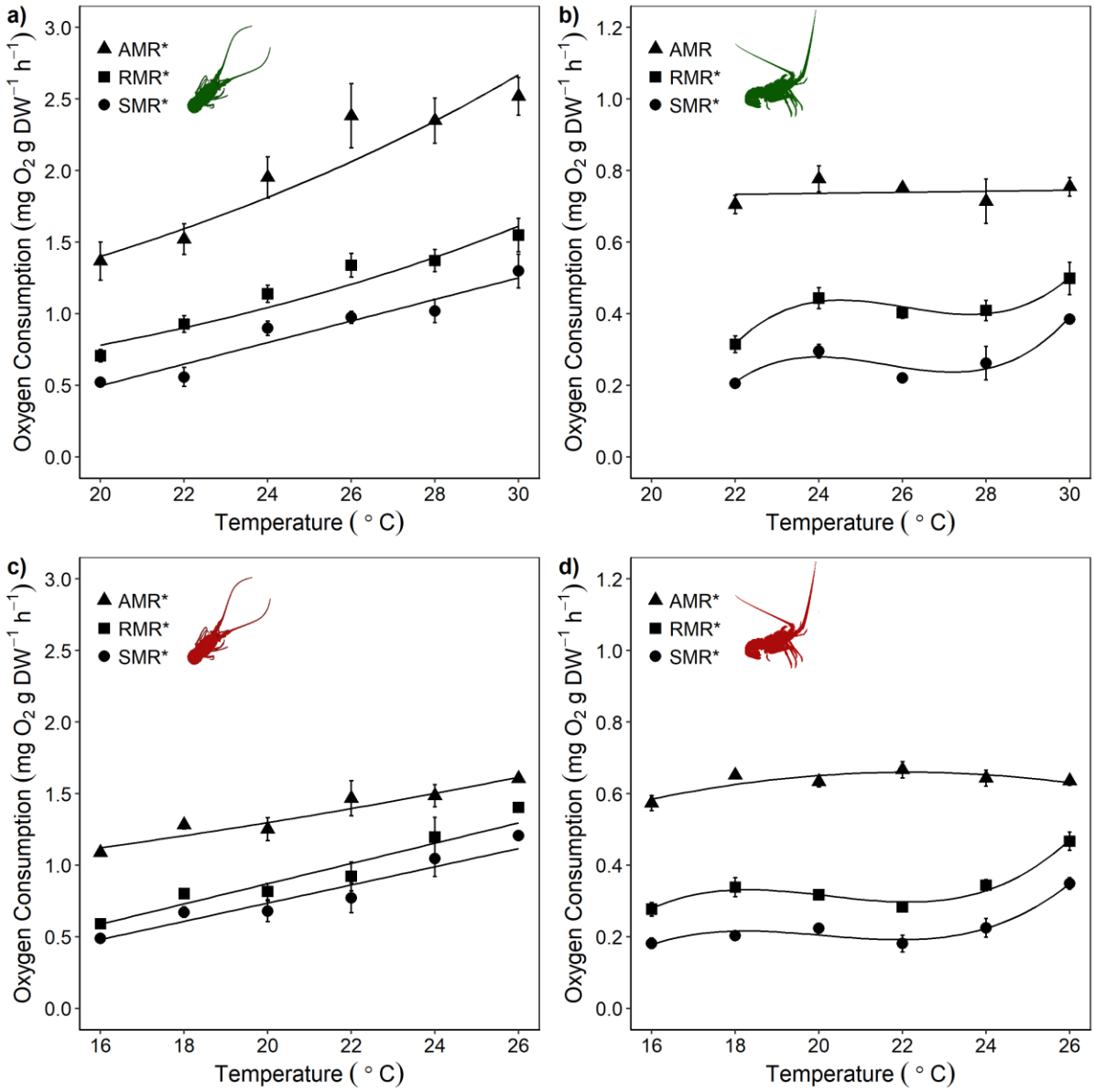

Figure 3.2. Active, routine and standard metabolic rates of *Sagmariasus verreauxi* and *Jasus edwardsii*. Results show a) *S. verreauxi* puerulus, b) *S. verreauxi* juveniles, c) *J. edwardsii* puerulus, and d) *J. edwardsii* juveniles. Metabolic rates noted in the legends are active metabolic rate (AMR), resting metabolic rate (RMR) and standard metabolic rate (SMR). Values are mean ± 1 SE. Sample size ranged from 4 to 10 individuals per temperature treatment. Significance at $\alpha = 0.05$ signified by * in legends. Details for regressions are provided in Table S3.1.

Aerobic scope measurements for all species and life stages exhibited quadratic relationships with temperature, and all showed significant changes in response to temperature except *Jasus edwardsii* puerulus (Regression model; $p = 0.057$, Figure 3.3, Table S3.1). There were significant differences between species and temperatures for aerobic scope of both puerulus and juveniles (GLM; Puerulus [Species $p = 0.010$, Temperature $p = 0.005$], Juvenile [Species $p < 0.001$, Temperature $p = 0.002$], Table 3.1).

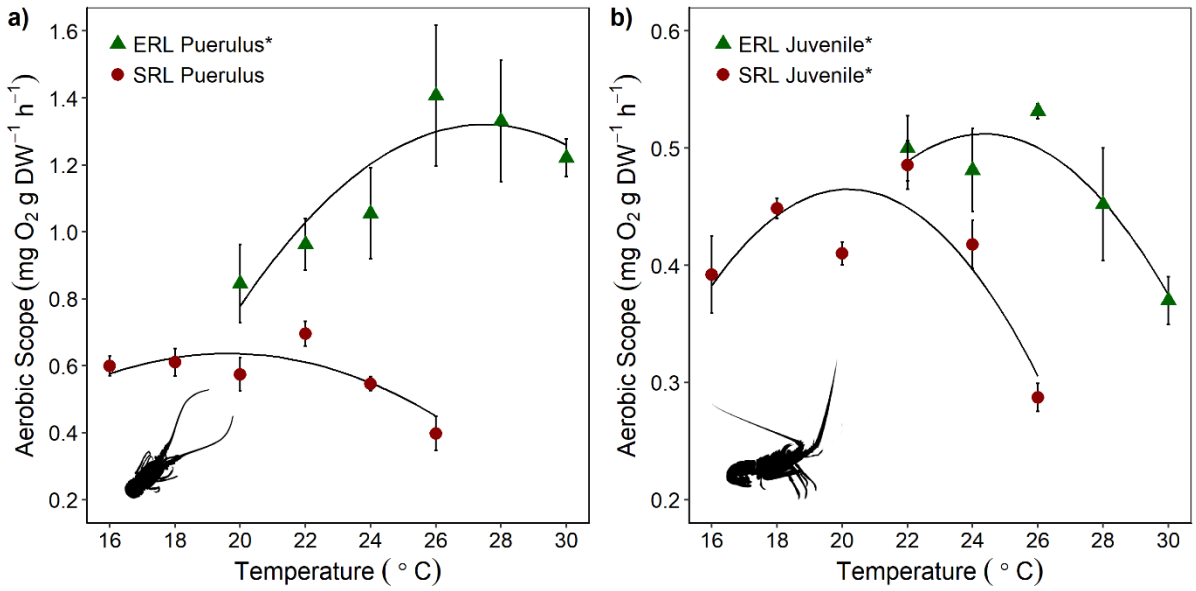

Figure 3.3. Aerobic scope of *Sagmariasus verreauxi* and *Jasus edwardsii*. Results show the a) puerulus and b) juvenile life stages, where *S. verreauxi* is shown as 'ERL' (green triangles) and *J. edwardsii* is shown as 'SRL' (red circles). Values are mean ± 1 SE. Sample size ranged from 4 to 10 individuals per temperature treatment. Significance at $\alpha = 0.05$ signified by * in legends. Details for regressions are provided in Table S3.1.

Only the *J. edwardsii* average escape speed relationships scaled significantly with temperature over the tested temperature ranges for both species and life stages (regression models; puerulus $p = 0.009$, juveniles $p < 0.001$, Figure 3.4, Table S3.1), though *S. verreauxi* puerulus relationships were near significant for both maximum and average escape speeds (regression

models; p = 0.053 and p = 0.053, respectively, Table S3.1). Maximum escape speed differed significantly between the two species at both life stages (GLM; Puerulus [Species p <0.001], Juvenile [Species p = 0.008], Table 3.1). There was also an interaction between species and temperature affecting maximum escape speed in juveniles (GLM; Juveniles [Species*Temperature p = 0.030], Table 3.1). *Jasus edwardsii* puerulus had only one replicate for escape speed measurements at 26°C due to sampling constraints and therefore was omitted from the escape speed analyses.

Table 3.1. Generalised linear model statistics of the effect of species (*Jasus edwardsii* and *Sagmariasus verreauxi*) and temperature on different thermal tolerance measures, aerobic scope and maximum escape speed at both life stages (puerulus and juvenile). The random effects error term accounts for the respirometry chamber. The 'Sp.*Temp.' indicates the species cross temperature interaction term in the model.

	Random effects			Fixed Effects				
Model	Factor	Variance	Std.Dev.	Factor	Estimate	Std. Error	t value	P value
Aerobic scope of puerulus	Chamber	0.000	0.000	Species	1.030	0.766	1.345	0.010*
				Temperature	0.067	0.020	3.373	0.005*
				Sp.*Temp.	-0.063	0.034	-1.843	0.065
Aerobic scope of juveniles	Chamber	<0.001	0.020	Species	-0.280	0.169	-1.658	<0.001*
				Temperature	-0.015	0.006	-2.489	0.002*
				Sp.*Temp.	0.007	0.007	1.031	0.303
Maximum escape speed of puerulus	Chamber	0.000	0.000	Species	-0.267	0.277	-0.962	<0.001*
				Temperature	-0.016	0.007	-2.189	0.130
				Sp.*Temp.	0.020	0.012	1.639	0.101
Maximum escape speed of juveniles	Chamber	0.001	0.036	Species	-0.853	0.481	-1.772	0.008*
				Temperature	-0.029	0.017	-1.761	0.850
				Sp.*Temp.	0.043	0.020	2.175	0.030*

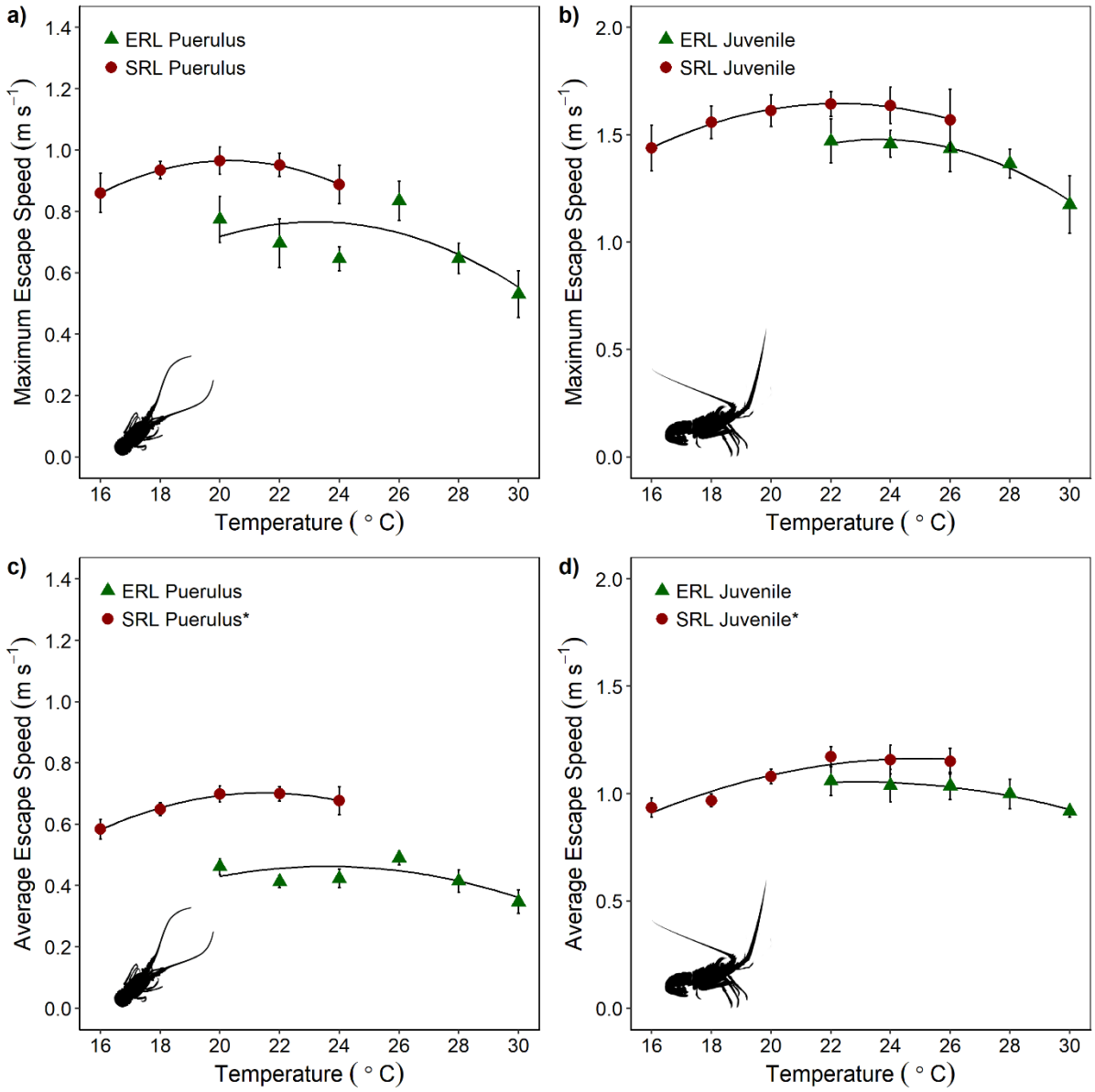

Figure 3.4. Maximum and average escape speeds of *Sagmariasus verreauxi* and *Jasus edwardsii*. Results show a) the maximum escape speed of the pueruli, b) the maximum escape speed of the juveniles, c) the average escape speed of the pueruli and d) the average escape speed of the juveniles, where *S. verreauxi* is shown as 'ERL' (green triangles) and *J. edwardsii* is shown as 'SRL' (red circles). Values are mean ± 1 SE. Sample size ranged from 4 to 10 individuals per temperature treatment. Significance at $\alpha = 0.05$ signified by * in legends. Details for regressions are provided in Table S3.1.

Thermal optima differed between species, life stage and measure of performance (Table 3.2, Figure 3.5). While the juvenile stages of each species showed similar thermal optima between the two measures of performance, the puerulus stages had differences in the thermal optimum between aerobic scope and maximum escape speed of 2-4°C. With the puerulus stage, the greatest difference in performance measure optima was recorded in *S. verreauxi* of ~4°C, compared to ~2°C for *J. edwardsii* puerulus. For *S. verreauxi*, the largest differences observed in the thermal optimum between life stages (puerulus and juveniles) was in aerobic scope optima (~3°C), while for *J. edwardsii*, the biggest thermal differences between life stages were with the maximum escape speed optima (2.4°C).

Table 3.2. Calculated thermal optima for two measures of performance for *Sagmariasus verreauxi* and *Jasus edwardsii*. Absolute difference (no sign) was calculated between the thermal optima to illustrate the match or mismatch between performance measures.

Species and life stage	Aerobic Scope	Maximum escape speed	Absolute difference
Sagmariasus verreauxi puerulus	27.5°C	23.2°C	4.3°C
Sagmariasus verreauxi juveniles	24.3°C	23.6°C	0.7°C
Jasus edwardsii puerulus	20.2°C	22.2°C	2.0°C
Jasus edwardsii juveniles	19.6°C	19.8°C	0.2°C

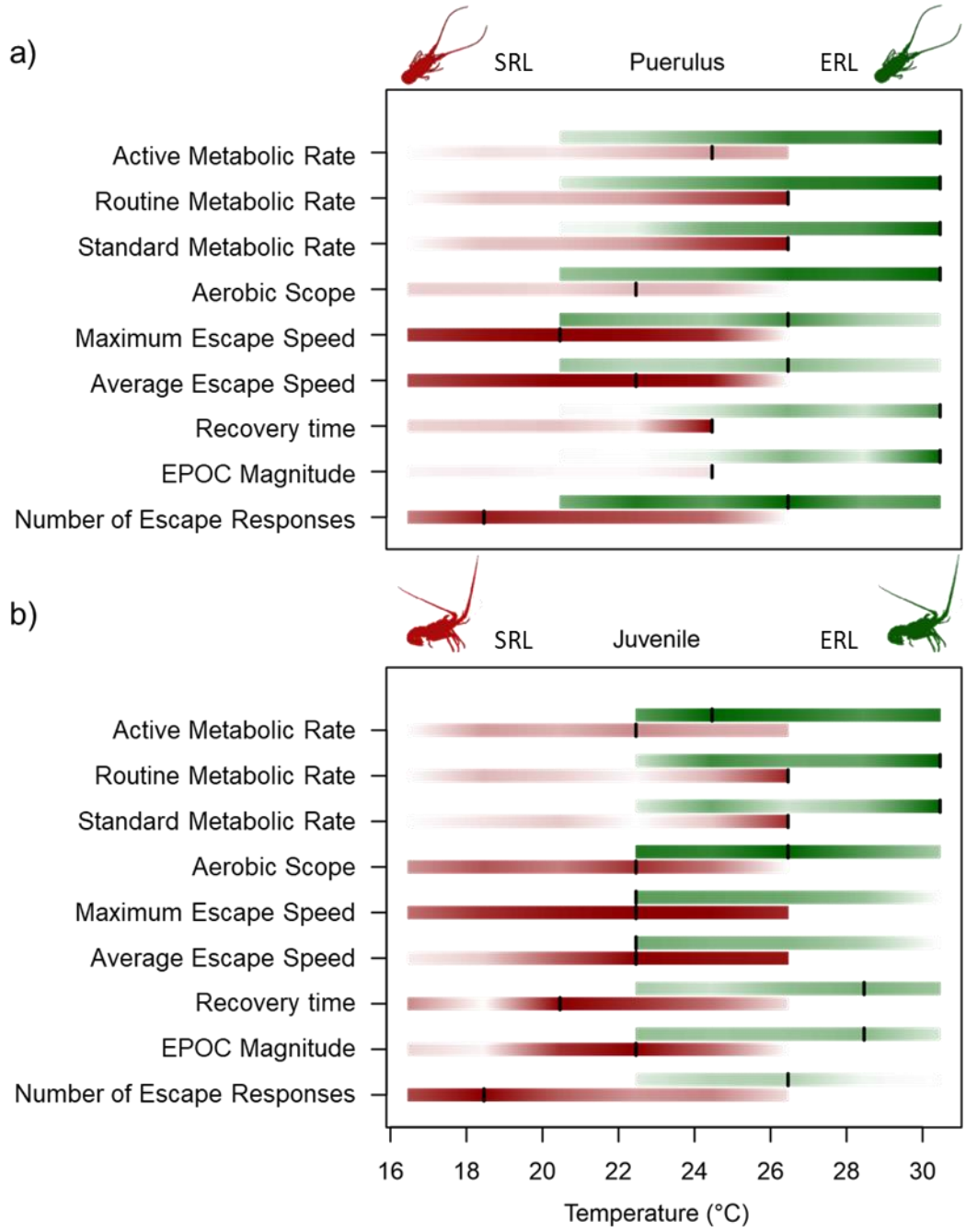

Figure 3.5. Comparison of thermal optima over a range of performance measures for *Jasus edwardsii* and *Sagmariasus verreauxi*. Here, a) shows the puerulus measures and b) the juvenile measures. In both plots, the red bars ('SRL' left aligned bars from 16-24°C or 16-26°C) signify *J. edwardsii* and the green bars ('ERL' right aligned bars from 20-30°C or 22-30°C), *S. verreauxi*. The intensity of the bar indicates the magnitude of performance where high intensity is a higher value. The black vertical bars indicate the temperature at which the highest value for each performance measure was achieved.

Time taken to recover back to oxygen consumption values within two standard deviations of resting metabolic rate followed exponential regression relationships for both species and life stages, however only the regression for *S. verreauxi* puerulus was significant (Figure S3.1, Table S3.1). Excess post-exercise oxygen consumption (EPOC) recovery measurements also followed exponential regression relationships for both species and life stages, again with only *S. verreauxi* puerulus having a significant relationship (Figure S3.2, Table S3.1). Results of Pearson correlation tests showed significant positive relationships between recovery time and the magnitude of EPOC for both species and life stages (Figure 3.6, *S. verreauxi* puerulus, $r(37) = 0.838$, $p < 0.001$, *J. edwardsii* puerulus, $r(29) = 0.668$, $p < 0.001$, *S. verreauxi* juveniles $r(19) = 0.913$, $p < 0.001$, and *J. edwardsii* juveniles, $r(32) = 0.794$, $p < 0.001$). The slope of the correlation indicates that it takes more energy to recovery from multiple escape responses for *S. verreauxi* puerulus than it does for *J. edwardsii* puerulus. This pattern was also observed in the juveniles however the magnitude of difference in the slope is less pronounced. Also note that the trials were stopped at 24 h post-exercise which accounts for the clustering of points around this time. These indicate the individuals that did not recovery to within two standard deviations of resting metabolic rate before the trials were completed.

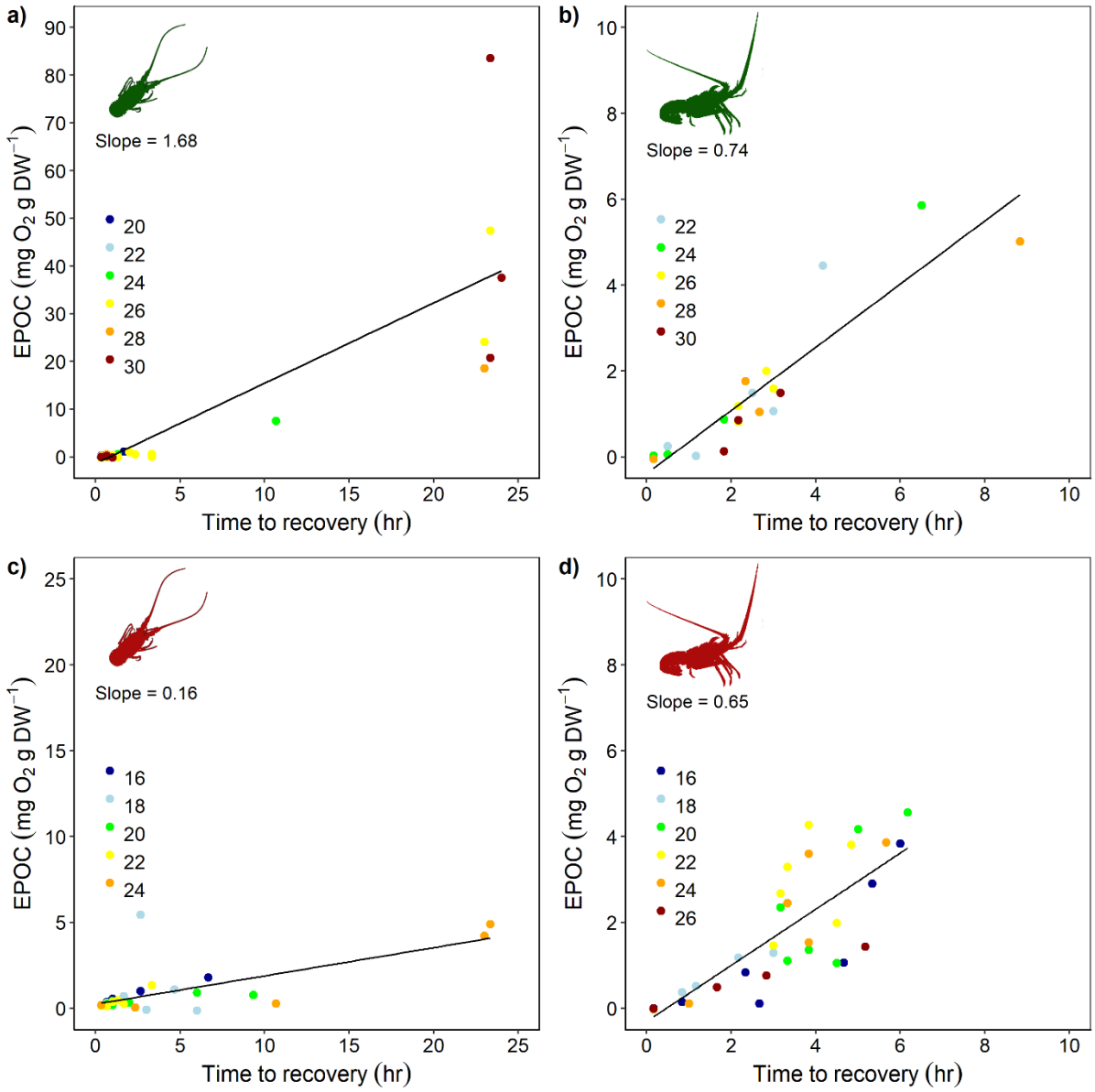

Figure 3.6. Correlation between recovery measures of time taken to recover and excess post-exercise oxygen consumption (EPOC Results show a) *S. verreauxi* puerulus, b) *S. verreauxi* juveniles, c) *J. edwardsii* puerulus and d) *J. edwardsii* juveniles. Slope value indicates the slope (m) of the regression line y = mx + c. Coloured points correspond to temperature treatment.

The number of escape responses (measured as the number of tail flick responses to stimuli) exhibited by both species and life stages scaled non-significantly with temperature, except for *J. edwardsii* juveniles that showed a significant linear decline in the number of escape responses as temperatures increased (Figure S3.3, Table S3.1). *Jasus edwardsii* juveniles also had significantly higher numbers of escape responses than *S. verreauxi* juveniles (Welch two sample t-test; $t(52.24) = 4.35$, $p < 0.001$). As for maximum and average escape speed regressions, *J. edwardsii* puerulus had only one replicate for number of escape responses at 26°C and was therefore omitted from the analyses.

Discussion

These experiments showed that thermal pattern, optima and magnitude of response vary between performance measure, life stage and species, and highlights that a single measure of performance does not predict whole organism performance (Norin et al. 2014, Sinclair et al. 2016, Fitzgibbon et al. 2017, Twiname et al. in review). This supports a coordinated assessment of multiple and life-stage specific thermal performance measures to identify performance attributes that are most appropriate to predict the effects of environmental change on species fitness, survival and distribution.

Mismatch of thermal optima between performance measure, life stage and species

As hypothesised, *S. verreauxi* displayed higher optimal temperatures for aerobic scope than the *J. edwardsii*, for both puerulus and juveniles (Figure 3.3). However, while *S. verreauxi* had higher optimal temperatures for escape speed (though due to non-significance the exact point of the optimal temperature is difficult to determine), the magnitude of both maximum and average escape speeds was higher in *J. edwardsii* than *S. verreauxi* across all tested temperatures, including those at which the species performances overlap (Figures 3.4 and 3.5).

In addition, performance measure optima also varied between life stages within species, where thermal optima were generally higher for puerulus than the juvenile stages (Table 3.1). Thermal response of performance traits differed also within the same species. *Sagmariasus verreauxi* thermal optima were higher for aerobic scope than escape speed, however this was the opposite for *J. edwardsii*, which had higher thermal tolerances for escape speed than aerobic scope. The observed variation of thermal optima across performance traits, life stage and species suggests; i) that temperatures for species optimal performance vary depending on which performance trait is most critical to a particular species, life stage and the predominant ecosystem pressure; ii) that a single measure of performance at a single life stage may not accurately predict whole animal performance over its entire life span and iii) that thermal history alone may be misleading to predict performance outcomes. Selection of experimental performance traits therefore requires careful consideration of the species' ecological setting and life stage to achieve more accurate estimates of climate driven distribution shifts.

Aerobic scope

Sagmariasus verreauxi had higher thermal optima for aerobic scope than *J. edwardsii* (Figure 3.3, Table 3.2). This likely reflects the different evolutionary thermal histories of both species, with *J. edwardsii* found in cooler temperate waters and *S. verreauxi* in warm-temperate to subtropical waters (Gardner et al. 2006, Montgomery et al. 2009). Aerobic scope has been proposed as a way to predict effects of ocean warming, however there is evidence for and against its use (Pörtner & Knust 2007, Clark et al. 2013, Pörtner et al. 2017, Jutfelt et al. 2018). While aerobic scope may not be a unifying principle for performance in all species, it is still a highly valuable measure of performance and can inform us of potential directions of performance change under ocean warming scenarios. Using this assumption, with continued ocean warming around Tasmania it is likely that *S. verreauxi* will further extend its range into southern Tasmania, as well as increase in abundance, as temperatures become more favourable

in terms of their aerobic scope. Warming will facilitate larval settlement of *S. verreauxi* puerulus in Tasmania, due to changing ocean currents and temperatures exceeding critical levels required to facilitate over-winter survival of newly settled puerulus and juveniles (Figueira et al. 2009, Cetina-Heredia et al. 2015).

Escape speed

While *S. verreauxi* have higher aerobic scope magnitudes and thermal optima than *J. edwardsii*, *J. edwardsii* exhibited faster escape speeds across most temperatures including at the crossover temperatures, which *J. edwardsii* may experience with further warming within its current distribution range (Figure 3.4). Faster escapes by *J. edwardsii* indicate significant ecological pressure on this trait during this early life stage. The spiny lobster life cycle is characterised by a long pelagic larval duration before puerulus undertake a costly swim from offshore to near coastal environments to settle into suitable habitats (Phillips et al. 2006). This settlement process is fraught with danger for puerulus that have to avoid the 'wall of mouths' phenomena that faces the larval stages of many different species recruiting into new environments (Emery 1973, Hamner et al. 1988). Therefore, escaping predator attacks during larval settlement is essential to recruit to and sustain a local population (Phillips et al. 2006). However, as it is likely that predator attack speeds are also likely to change with warming, the way temperature affects the outcome of predator-prey interactions is likely complex (Dell et al. 2014, Lord et al. 2017). From this study we can deduce that as *J. edwardsii* puerulus have the potential to escape faster than *S. verreauxi*, they possess a competitive advantage that may influence settlement and recruitment success of the species.

Aerobic versus anaerobic performance traits

The discrepancy of thermal optima between aerobic scope and escape speed may be explained by their vastly different power mode. Aerobic scope is purely supported by aerobic energy provision, taking place in mitochondria that produce ~1.5-2.5 adenosine triphosphate (ATP)

molecules per consumed oxygen molecule via oxidative phosphorylation (Hinkle 2005). Aerobic scope reflects a complex composition of numerous oxygen dependent sub-processes from the cellular up to the systemic level (Pörtner 2002). Consequently, as a high-level performance trait, thermal tolerance of aerobic scope results from the cumulative interaction of thermal tolerances of each of these sub-processes, forming an overall thermal tolerance curve which is more constrained than its individual sub-processes. In contrast, escape bursts by decapod crustaceans or fishes, are mainly powered by anaerobic white muscle (De Zwaan & v.d. Thillart 1985). Here ATP is derived from ATP stored in the form of phosphoarginine (in crustaceans) as well as by converting glycogen to lactate by anaerobic glycolysis (England & Baldwin 1983, Speed et al. 2001). Phosphoarginine powers the first strong burst followed by weaker burst, which are sustained by glycolysis. This process is strictly time limited until phosphoarginine and glycogen stores are exhausted, and muscles become too acidic to operate (England & Baldwin 1983). Anaerobic white muscle bursts can be considered as a low-level performance trait, as it is largely driven by cellular enzyme reactions and cellular substrate diffusion. Low level cellular processes are less complex and therefore considered to operate at broader temperature scales (Pörtner, 2002), and if not constrained by generic body functions, will determine the overall animal response. This would explain why optimal temperature for escape bursts of spiny lobsters divert from those of aerobic scope, as well as why escape bursts (i.e. escape speed and number of escape response, Figures 3.4 and S3.3) show very little response to temperature changes within the measured temperature range.

Links between opposing performance traits

Different biological processes and thus ecological outcomes of aerobic scope and escape burst are independent from each other. However, escape capacity becomes dependent on aerobic scope, following bursts, during recovery when phosphate and glycogen stores need to be refilled and accumulated lactate and protons to be removed using energy (ATP) supplied from

aerobic metabolism (c.f. oxygen debt, (Head & Baldwin 1986, Morris & Adamczewska 2002)). In this case, aerobic scope defines if and how fast anaerobic energy stores can be recharged, and consequently how frequent animals can face recurring predator attacks.

These results showed that recovery following escape bursts varies in both time and the amount of oxygen required to pay off the oxygen debt (excess post-exercise oxygen consumption = EPOC) between individuals within temperature treatments. Recovery in juvenile spiny lobsters did not differ between *J. edwardsii* and *S. verreauxi* and showed a gradual distribution of recovery rates among individuals, indicating that juvenile spiny lobsters of both species exhibit similar capacity recover from escape responses as a result of predation. Similarly, many puerulus of *J. edwardsii* and *S. verreauxi* recovered within similar time frames. However, puerulus exposed to high temperatures divided into individuals that either recovered quickly (in less than 3 hours) or did not recover for the full 24h of trials, with this result most pronounced in *S. verreauxi* (Figures 3.5 and S3.1). This suggests that the individuals that recover their oxygen debt more quickly, might be less susceptible to predation at higher temperatures than others, driving selection of this particular phenotype (Foo & Byrne 2016, Clark et al. 2017). Further, *S. verreauxi* required disproportionally more oxygen to recover its oxygen debt at higher temperatures than *J. edwardsii* (Figure 3.6). This indicates a stronger reliance of *S. verreauxi* pueruli on aerobic scope and sufficient ambient oxygen levels at higher temperatures. These differences in individual responses indicate high intra- and moderate inter-specific variation among spiny lobsters, which implies opportunity for natural selection to favour phenotypes better adapted to warming oceans (Foo & Byrne 2016, Clark et al. 2017).

Predicting range shifts and species' interactions

For both measures of performance, and both life stages, temperatures can be identified where the thermal performance curves of the two species cross over. However, due to the variation between performance measures and life stages, predicting a single temperature where overall

animal performance may decline or increase, and hence the outcomes of interactions may change, is challenging. Comparing the thermal performance curves of two or more species may allow us to make general predictions of how species relative performances may change under warming. However, comparing these curves alone will not elucidate indirect effects of species interactions. In future, physiological mechanisms can be incorporated into mechanistic models to provide a more complete and robust prediction of future changes for species under future climate scenarios (Evans et al. 2015).

Limitations

Conclusions from this study are limited by the following aspects. First, thermal tolerances presented here are indicative of short-term, acute temperature changes and do not necessarily reflect changes in performance over longer time periods where species plasticity and acclimation may mitigate the negative effects of a warming environment. This said, these results are more relevant to shorter-term warming events such as marine heatwaves. In recent decades, marine heatwaves have increased in number in south-east Australia, including a particularly strong event over the Austral summer of 2015/16 (Oliver et al. 2017, Oliver et al. 2018). This trend is likely to continue in the future (Oliver et al. 2018) and the results from a short time-scale experiment presented here might be indicative of changes observed as a result of a heatwave event. The second is that thermal performance curves do not incorporate other aspects such as mortality rates during the derivation of the curves. For example, *S. verreauxi* puerulus had the highest thermal tolerances of the study at ~27°C for aerobic scope. However, this trial also observed the highest mortality rate of 5 individuals (1, 1 and 3 mortalities at 26, 28 and 30°C treatments, respectively). Thus, caution should be used when interpreting thermal tolerance results as not all measures are representative of the overall performance of a whole group of individuals. Thirdly, due to supply constraints, some experimental trials had few replicates due to the unavailability of enough individuals, for example access to *S. verreauxi*

juveniles was limited, resulting in fewer replicates per temperature and fewer temperature treatments. Finally, this study is constrained by *S. verreauxi* individuals being bred at the IMAS aquaculture facility while *J. edwardsii* were wild-caught. This may introduce bias in that *S. verreauxi* individuals were not subject to any predation pressure during their early life stages. This may also indicate that performance for this species may be underestimated as the tested individuals have not had to survive predation through their larval and settlement stages, thereby not having the most successful individuals remaining as would be the case for *J. edwardsii*. However, as intra-specific variation was still high, we can assume that we have captured an accurate representation of effects of temperature on measures of performance in *S. verreauxi*.

Conclusion

In summary, thermal optima vary between performance measure, life stage and species. The data emphasize that it is critical to evaluate multiple performance measures, relevant to the specific ecosystem pressure during developmental ontogeny, to better predict the effects of environmental change on species fitness, survival and distribution. It was found that *S. verreauxi* have higher aerobic scope measurements than *J. edwardsii*, indicating that with continued warming in south east Australia, particularly in Tasmania, *S. verreauxi* have the thermal capacity to expand their range and increase in abundance. However, *J. edwardsii* had faster escape speeds and can potentially avoid predation better than *S. verreauxi* at common crossover temperatures. The relative impact of aerobic scope and predator escape capacity will vary with life stage (e.g. larvae, adult) and specific ecosystem pressure (e.g. predator abundance). Temperature projections to 2100 in Tasmania reach 22°C in the north, a temperature at which the aerobic scope of *J. edwardsii* is declining. Therefore, any changes to the outcome of a potential interaction and hence changes to population dynamics may become apparent. However, these predictions may also change depending on the selected performance measure, with predictions using aerobic scope indicating that performance of *S. verreauxi* is

maximised at higher temperatures, but not for escape speed. While thermal performance curves are very useful in illustrating how a single species may react to warming, they may not reveal the potential indirect effects of changing species interactions that might occur. Incorporating thermal performance data into modelling approaches may be able to elicit some of these indirect effects that are not clearly seen or predicted using individual species thermal performance curves. Future studies should try to directly quantify the outcomes of a direct interaction between the local and range-shifting species to determine if measures of individual thermal tolerances can predict changes in species interactions under future ocean warming scenarios.

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Supplementary materials

Table 3.1. Results of regression analyses of different performance responses to temperature of *Sagmariasus verreauxi* (ERL) and *Jasus edwardsii* (SRL). Analyses in the form of linear ($y = ax + b$), exponential ($y = e^{a+bx}$), quadratic ($y = ax^2 + bx + c$) and polynomial ($y = ax^3 + bx^2 + cx + d$) regressions. * indicates significance at $p < 0.05$.

	Regression	a	b	c	D	R^2	F-statistic	df	p
Standard metabolic rate									
ERL Puerulus	Linear	0.075	-1.010	-	-	0.586	62.360	44	0.000*
ERL Juveniles	Polynomial	0.003	-0.199	5.063	-42.600	0.523	6.576	18	0.003*
SRL Puerulus	Linear	0.064	-0.536	-	-	0.535	35.680	31	0.000*
SRL Juveniles	Polynomial	0.001	-0.059	1.180	-7.557	0.659	20.600	32	0.000*
Routine metabolic rate									
ERL Puerulus	Exponential	0.073	-1.700	-	-	0.633	75.720	44	0.000*
ERL Juveniles	Polynomial	0.003	-0.207	5.390	-46.100	0.541	7.062	18	0.002*
SRL Puerulus	Linear	0.071	-0.544	-	-	0.591	44.740	31	0.000*
SRL Juveniles	Polynomial	0.001	-0.074	1.477	-9.459	0.674	22.060	32	0.000*
Active metabolic rate									
ERL Puerulus	Exponential	0.064	-0.952	-	-	0.485	41.350	44	0.000*
ERL Juveniles	Linear	0.001	0.702	-	-	0.002	0.049	20	0.828
SRL Puerulus	Exponential	0.036	-0.468	-	-	0.425	22.140	30	0.000*
SRL Juveniles	Quadratic	-0.002	0.088	-0.319	-	0.258	5.746	33	0.007*
Aerobic scope									
ERL Puerulus	Quadratic	-0.010	0.531	-5.983	-	0.148	3.738	43	0.032*
ERL Juveniles	Quadratic	-0.004	0.209	-2.032	-	0.300	4.066	19	0.034*
SRL Puerulus	Quadratic	-0.005	0.181	-1.139	-	0.179	3.166	29	0.057
SRL Juveniles	Quadratic	-0.005	0.190	-1.451	-	0.514	17.420	33	0.000*
Time to recovery									
ERL Puerulus	Exponential	0.184	-4.407	-	-	0.1638	7.248	37	0.011*
ERL Juveniles	Exponential	0.069	-1.323	-	-	0.029	0.571	19	0.459
SRL Puerulus	Exponential	0.085	-1.039	-	-	0.041	1.229	29	0.277
SRL Juveniles	Exponential	0.007	0.637	-	-	0.000	0.016	32	0.901
Excess post-exercise oxygen consumption									
ERL Puerulus	Exponential	0.308	-8.280	-	-	0.1779	6.491	30	0.016*
ERL Juveniles	Exponential	0.102	-2.922	-	-	0.034	0.605	17	0.447
SRL Puerulus	Exponential	-0.043	0.136	-	-	0.012	0.328	27	0.571
SRL Juveniles	Exponential	0.130	-2.538	-	-	0.096	3.067	29	0.090
Maximum escape speed									
ERL Puerulus	Quadratic	-0.005	0.214	-1.720	-	0.131	3.154	42	0.053
ERL Juveniles	Quadratic	-0.007	0.331	-2.434	-	0.238	2.960	19	0.076
SRL Puerulus	Quadratic	-0.006	0.232	-1.387	-	0.117	1.857	28	0.175
SRL Juveniles	Quadratic	-0.005	0.235	-0.968	-	0.097	1.776	33	0.185
Average escape speed									
ERL Puerulus	Quadratic	-0.002	0.118	-0.926	-	0.131	3.158	42	0.053
ERL Juveniles	Quadratic	-0.003	0.120	-0.328	-	0.105	1.118	19	0.348
SRL Puerulus	Quadratic	-0.004	0.172	-1.149	-	0.288	5.669	28	0.009*
SRL Juveniles	Quadratic	-0.003	0.158	-0.804	-	0.393	10.670	33	0.000*
Number of escape responses									
ERL Puerulus	Quadratic	-0.149	7.411	-80.008	-	0.053	1.206	43	0.310
ERL Juveniles	Quadratic	-0.250	12.460	-141.113	-	0.108	1.154	19	0.337
SRL Puerulus	Linear	-0.009	10.503	-	-	0.000	0.001	29	0.983
SRL Juveniles	Linear	-1.314	47.989	-	-	0.349	18.230	34	0.000*

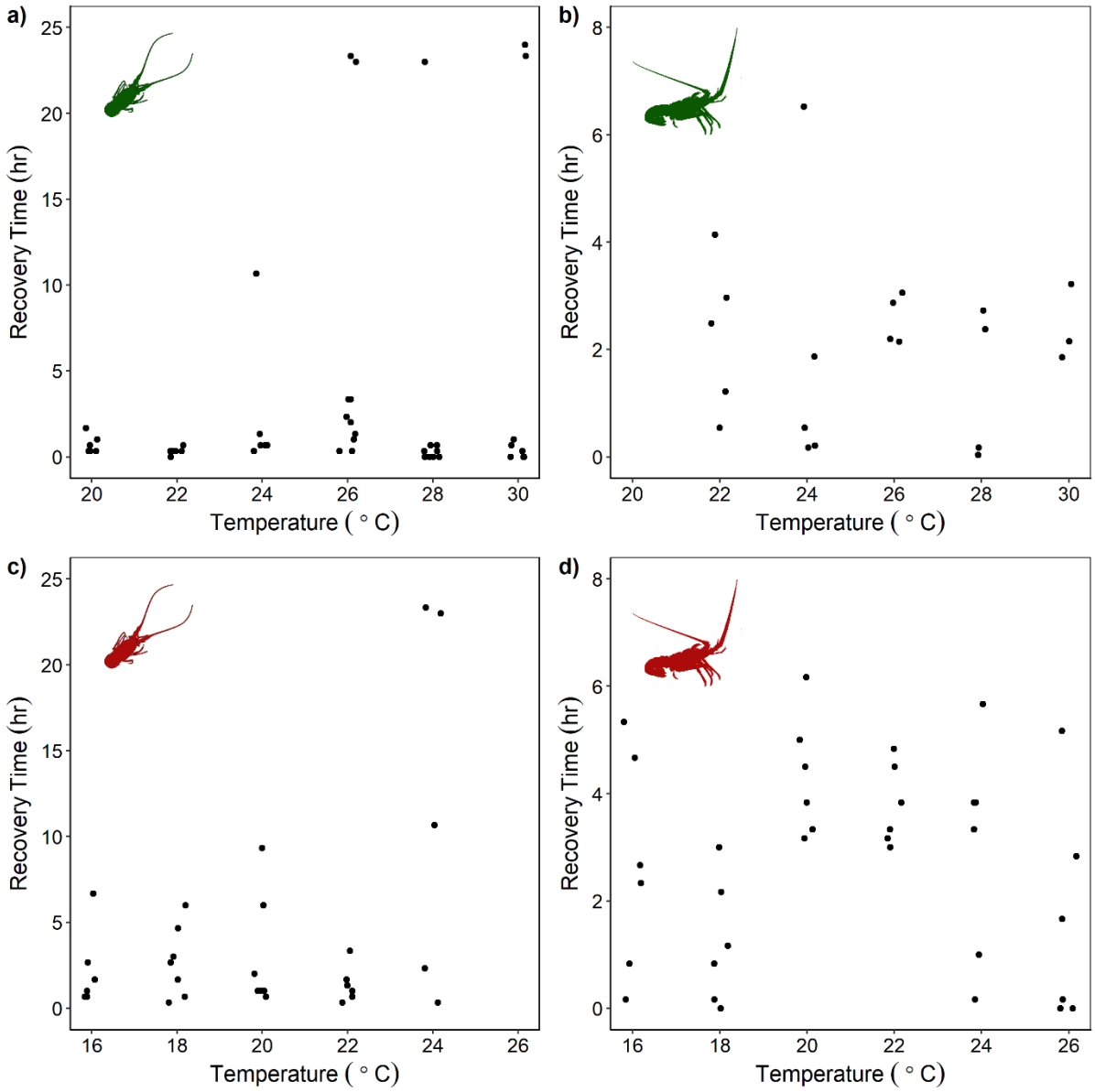

Figure S3.1. Time to recovery. Recovery is calculated as the return time to two standard deviations of routine metabolic rate after exercise for a) *Sagmariasus verreauxi* puerulus, b) *S. verreauxi* juveniles, c) *Jasus edwardsii* puerulus and d) *J. edwardsii* juveniles. Values are mean ± 1 SE. Sample size ranged from 4 to 10 individuals per temperature treatment. Details for regressions are provided in Table S3.1.

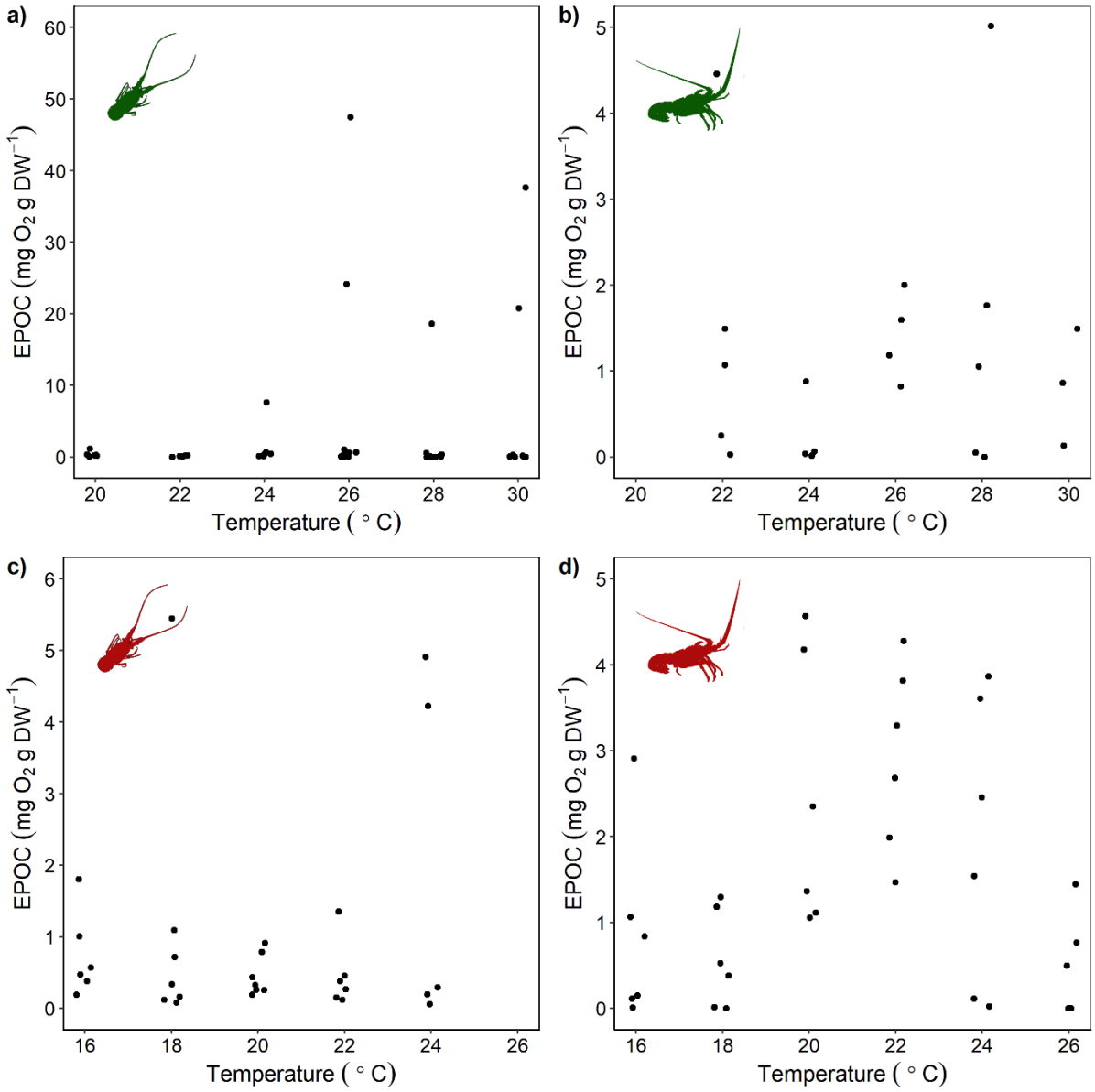

Figure 3.2. Excess post-exercise oxygen consumption (EPOC). Grid plots are of a) *Sagmariasus verreauxi* puerulus, b) *S. verreauxi* juveniles, c) *Jasus edwardsii* puerulus and d) *J. edwardsii* juveniles. Values are mean ± 1 SE. Sample size ranged from 4 to 10 individuals per temperature treatment. Details for regressions are provided in Table S3.1.

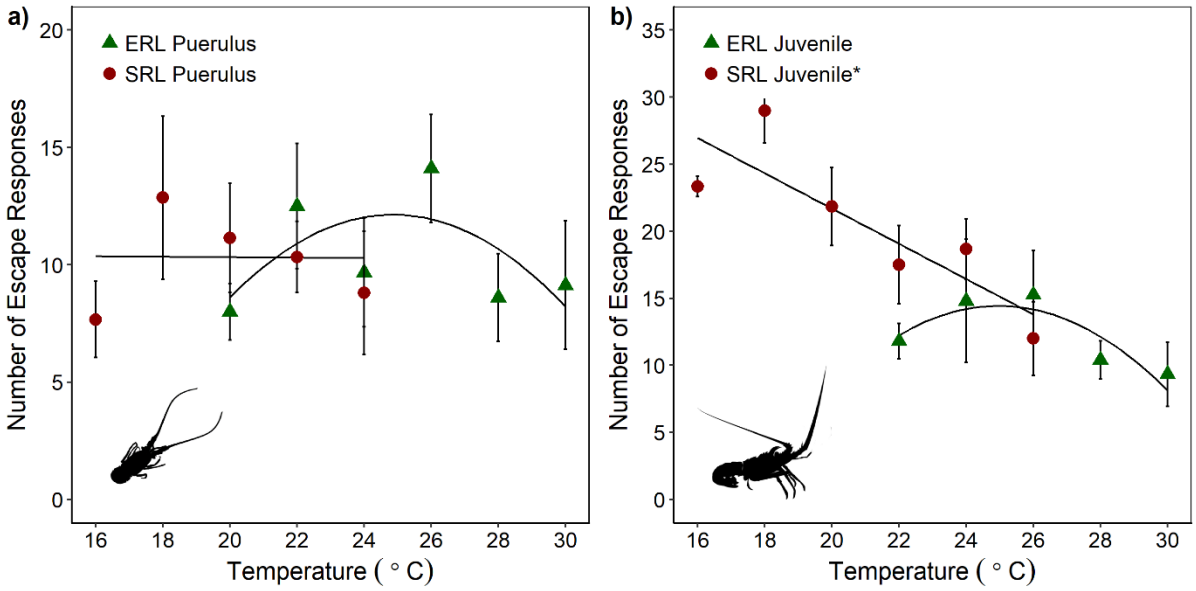

Figure 3.3. Number of escape responses for *Sagmariasus verreauxi* and *Jasus edwardsii*. Number of responses were measured as the number of tail flick responses to stimuli. Results show the a) puerulus and b) juvenile life stages, where *S. verreauxi* is shown as 'ERL' (green triangles) and *J. edwardsii* is shown as 'SRL' (red circles). Values are mean ± 1 SE. Sample size ranged from 4 to 10 individuals per temperature treatment. Significance at $\alpha = 0.05$ signified by * in legends. Details for regressions are provided in Table S3.1

CHAPTER 4

Interspecific competition for food between a resident and a range-shifting lobster species in marine warming hotspot.

Abstract

Species redistributions are one of the most prevalent changes being observed in oceans worldwide as a result of climate change. These 'range shifts' have the potential to alter species interactions and in turn affect community and ecosystem structure and functioning. One of the associated challenges is being able to predict temperature-driven changes to species interactions and the outcome of these changes for marine communities due to the complex and unpredictable nature of indirect effects. In the ocean warming hotspot of south-east Australia, many species have been observed shifting their ranges polewards. The eastern rock lobster, *Sagmariasus verreauxi* has extended its range into Tasmanian waters inhabited by the local southern rock lobster, *Jasus edwardsii*. Resource sharing may lead to altered competitive interactions between these lobster species in a new environment. Using video monitoring, competition of the two species for food resources at 18°C, 21°C and 24°C was investigated. In 80% of trials, behavioural competition was observed between the species. *Jasus edwardsii* succeeded in 84% of the total feeding trials where competition was observed, exhibiting significantly higher numbers of aggressive behaviour at all temperatures. This indicates that *J. edwardsii* is not only more competitive than the range shifting *S. verreauxi*, but also sustains competitive dominance at temperatures above previously examined physiological thermal optimums. Further, increasing competitive behaviours at 21°C and 24°C in both species indicate that temperature modulates the intensity of behavioural competition. These results suggest that outcomes of species interaction may not necessarily be inferred from thermal tolerance data alone and are influenced by factors such as behavioural phenotype or the capacity to sustain behaviour despite increasing performance limitations.

Keywords: *climate change, competition,* Jasus edwardsii, *range shift,* Sagmariasus verreauxi, *species interaction, species redistribution*

Introduction

Anthropogenic climate change is affecting marine ecosystems worldwide, resulting in altered physical and biological parameters (Doney et al. 2012). One of the most pervasive effects resulting from ocean warming are alterations to species' geographical ranges, or 'range shifts' (Parmesan & Yohe 2003, Poloczanska et al. 2013). While warming may directly affect individual species' performances, it will also have indirect effects through changes in species interactions (Kordas et al. 2011). Species interactions are important factors in determining the structure and functioning of marine ecosystems and changes to these interactions via range shifts may have important implications for marine ecosystems now and in the future (Winder & Schindler 2004, Kordas et al. 2011, Milazzo et al. 2013).

Competitive interactions are important factors in the structure and functioning of marine communities (Dayton 1971). Temperature-driven changes to competitive interactions may arise in different ways, including via changes in individual species performance or abundance in a way that alters the outcome of an interaction (Milazzo et al. 2013). There may also be the formation of novel species' interactions, as new species arrive in a new environment. Predicting changes to species interactions, and their potential subsequent influences on marine communities is one of the biggest challenges in climate change ecology (Lord et al. 2017). This is largely because the indirect effects, e.g. competitive release of species, resulting from changes to species interactions are complex and often unpredictable and have hence not been as readily studied as the direct effects of change, i.e. physiological changes (Lord et al. 2017).

The outcomes of competitive interactions can be dependent on a wide range of factors and hence there are potentially many performance measures that could be used to predict competitive strength or ability. Physiological parameters, such as aerobic metabolism, have been shown to predict competitive ability, and hence outcome of interspecific interactions (Seth et al. 2013, Killen et al. 2014). The size of competing organisms can also be a dominant factor

in the outcome of competitive interactions, such as between invasive green crab (*Carcinus maenas*) and native American lobster (*Homarus americanus*) (Williams et al. 2009). In competitive trials, only large sized American lobster outcompeted the green crab for food resources, while small and medium sized lobster were unable to dominate and spent more time seeking shelter. Aggression is another factor that influences the outcome of competitive interactions. In studies with hermit crabs competing for food resources, those individuals that were more aggressive were more likely to obtain the food items (Tran et al. 2014, Greggor & Laidre 2016). In fish, a local snapper species in the Gulf of Mexico has been shown to become more aggressive in the presence of range-shifting conspecifics (Marshak & Heck 2017). The different potential indicators of the outcomes of competitive interactions further illustrates the complex nature of species interactions and the difficulty in predicting the outcomes of such interactions.

In south-east Australia, many species have extended their ranges in response to ocean warming (Pitt et al. 2010, Last et al. 2011, Sunday et al. 2015). One of these is the eastern rock lobster, *Sagmariasus verreauxi* (Robinson et al. 2015). This range shifting species is currently increasing abundance in areas historically dominated by southern rock lobster, *Jasus edwardsii*. How these two species interact currently and under future ocean warming is unknown, though it is likely that the two species will undergo some form of direct or indirect competition due to similar resource requirements (Booth 2006, Byrne & Andrew 2013, Jeffs et al. 2013). As *J. edwardsii* is a valuable commercial species, understanding how these two species may interact, the outcome of that interaction, and changes with future warming, is critical for the adaptive management of the local fishery and ecosystems.

The aim of this study was to investigate competition for food between the two lobster species – the resident and the range-shifter – under different temperature regimes. It was hypothesized that individual species competitive ability will match thermal tolerance windows previously

investigated for these species (Twiname et al. in prep). Therefore, it is expected each species will be more competitive at their respective physiological optimal temperature range i.e. ~19-22°C for *J. edwardsii* and ~23-27°C for *S. verreauxi*.

Methods

Competitive interaction trials for food were conducted at three temperature treatments that encompass current and future ocean temperatures off Tasmania, 18 (n = 21), 21 (n = 18) and 24°C (n = 15), between size-matched individuals of *J. edwardsii* and *S. verreauxi*. Different sample sizes between temperature treatments were due to some trials having to be excluded due to moulting immediately before, after or during competitive trials. Competitive interactions were filmed when a food item was introduced to the tank and scored for the number of aggressive and submissive behaviours exhibited by both species, as well as the 'winner' of the interaction (individual that consumed the food).

Animal collection and holding

Adult *J. edwardsii* (n = 18, 298.85 ± 11.95 (mean ± standard deviation) mm total length) were collected in February 2017 using baited lobster pots in the Taroona Waters reserve (42.95 S, 147.35 E), south-eastern Tasmania. Adult *S. verreauxi* were purchased from commercial rock lobster fishermen operating along the east coast of Tasmania, from February to April 2017 (n = 18, 304.17 ± 15.87 mm total length). All lobsters were transported live to the Institute of Marine and Antarctic Studies (IMAS) aquaculture facility and held in 5000 L tanks supplied with flow-through raw seawater. The lobsters were separated by species to limit any interaction between them prior to experimentation. Each individual was tagged in the abdomen using a unique identification number T-bar tag (to prevent the tag being shed upon moulting), as well as a larger identification number attached to the carapace for easy identification in the tanks to reduce handling stress of the lobsters. Of the 18 individuals of each species, 10 were female

and 8 were male. For *J. edwardsii*, 6 of the 10 females were berried (carrying eggs). Due to biological differences between the species (*J. edwardsii* growing to smaller overall sizes, and hence smaller sizes at maturity), no *S. verreauxi* of similar size were berried.

Measurements of the lobsters upon introduction to the tanks were taken, including carapace length and width, total length and weight. The number of missing appendages (antennae and legs) were also recorded. The lobsters were fed 2-3 times per week with fresh or thawed blue mussels (*Mytilus galloprovincialis*) or thawed squid tentacles (*Loligo sp*.). Prior to the competitive trials, similar sized pairs (within 5mm of total length) of *J. edwardsii* and *S. verreauxi* were selected. Pairs of the same sex were selected using total length and weight as well as matched where possible in terms of missing appendages to eliminate any effect these losses may have had on behaviour. The four lobsters of each species from the selected pairs were transferred into two 175 L, 800 mm diameter round acclimation tanks, species separated, until the competition trials commenced i.e. four *J. edwardsii* were acclimated together in one tank, and four *S. verreauxi* were acclimated together in separate tank, to make sure no dominance structures between paired individuals of both species were developed before trials (see Figure 4.1). Tanks were supplied with flow-through filtered sea water, an air stone and a submersible heater (Carel ir33, Italy) to adjust and maintain tank temperatures. Two large concrete hides with enough space for all the individuals were also placed on opposite sides of the tank to provide shelter (Figure 4.1). A maximum of four same species individuals were acclimated at the same time in each acclimation tank and were fed with fresh or thawed blue mussels to excess every day in the afternoon. Any food not eaten was removed the next morning to prevent fouling of the water. Temperatures were increased by 1°C per day from ambient conditions until the trial temperature was achieved. The lobsters were left for seven days to acclimate to this temperature. Prior to the competition trials beginning, the lobsters were fasted for a period of 72 hours (deemed a suitable time from pilot fasting trials) to ensure

that the lobsters would compete for a food item in the trials. During the experimental trials, a 12h:12h light:dark regime was simulated.

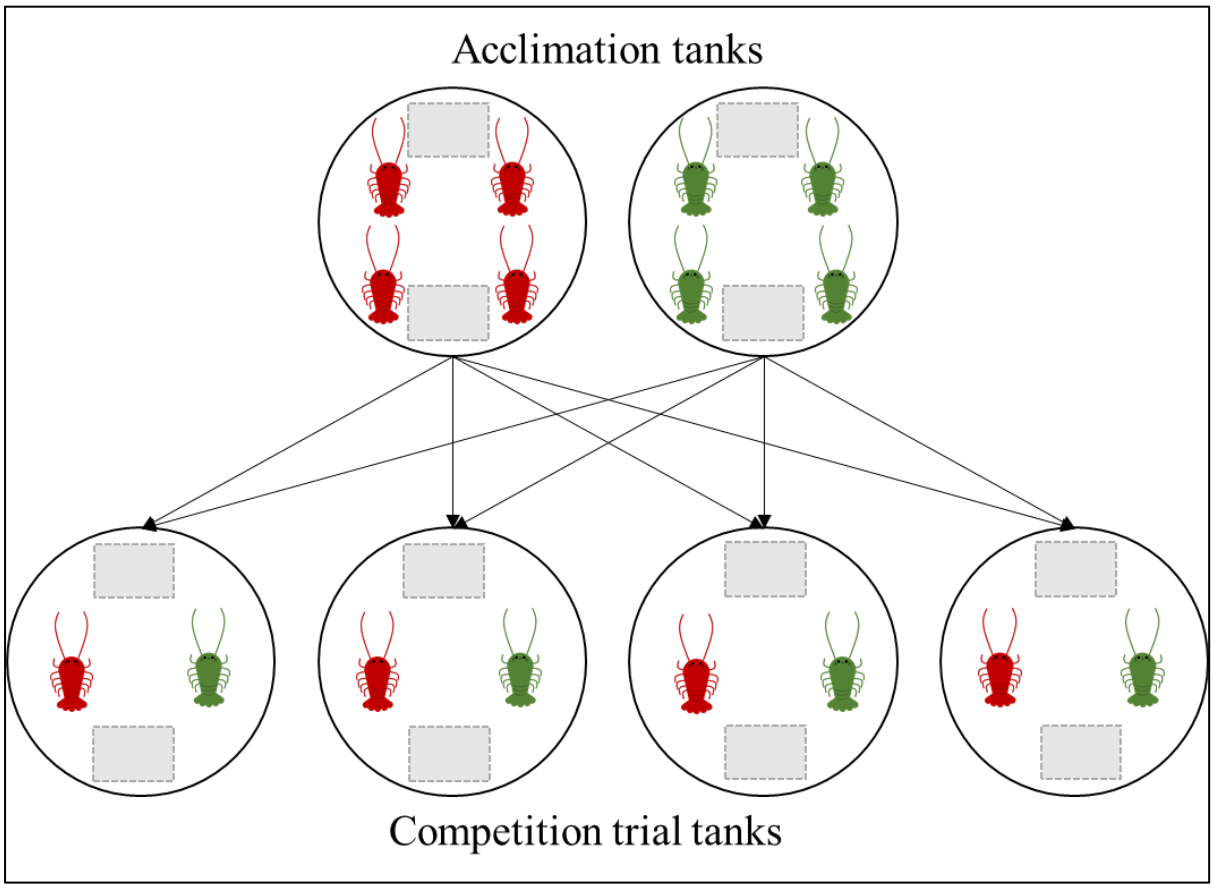

Figure 4.1. Experimental design of the competition experiments. Up to four individuals of each species (red lobsters = *Jasus edwardsii*, green lobsters = *Sagmariasus verreauxi*) were acclimated to trial temperatures in species separated acclimation tanks for one week before being transferred into competition tanks in their size-matched pairs (one of each species). Each of the tanks was supplied with flow-through filtered seawater, an air stone for aeration and circulation, and two concrete shelters (grey boxes).

Competition trials

Competition trials were conducted in 175 L, 800mm diameter tanks supplied with flow-through filtered sea water, an air stone and two concrete hides placed on either side of the tank. From the two acclimation tanks, size-matched pairs of *J. edwardsii* and *S. verreauxi* were introduced into four separate competition tanks 24 hours before feeding trials began to allow them to

acclimate to their new environment (Figure 4.1). No food was provided in during this 24 h period. After this 24 h, one half shell mussel was placed into the tank, approximately half way between the two lobsters. The trial was then filmed for 1 h. If neither lobster ate the mussel in that time, the mussel was removed. If the mussel was consumed, the empty shell was removed. Each size-matched pair of lobsters was only used for one competition trial that lasted 72 h, resulting in each pair of lobsters having three replicates, one per 24 h. Competition trials were conducted in the late afternoon under red light (see Figure 4.2), simulating dark conditions as lobsters are generally forage at night (Childress & Jury 2006). The air stones were removed while the competition trials were filmed as the disturbance to the water surface made identifying lobster activity difficult. They were re-introduced immediately after the trials and the tanks received constant water flow throughout the trial.

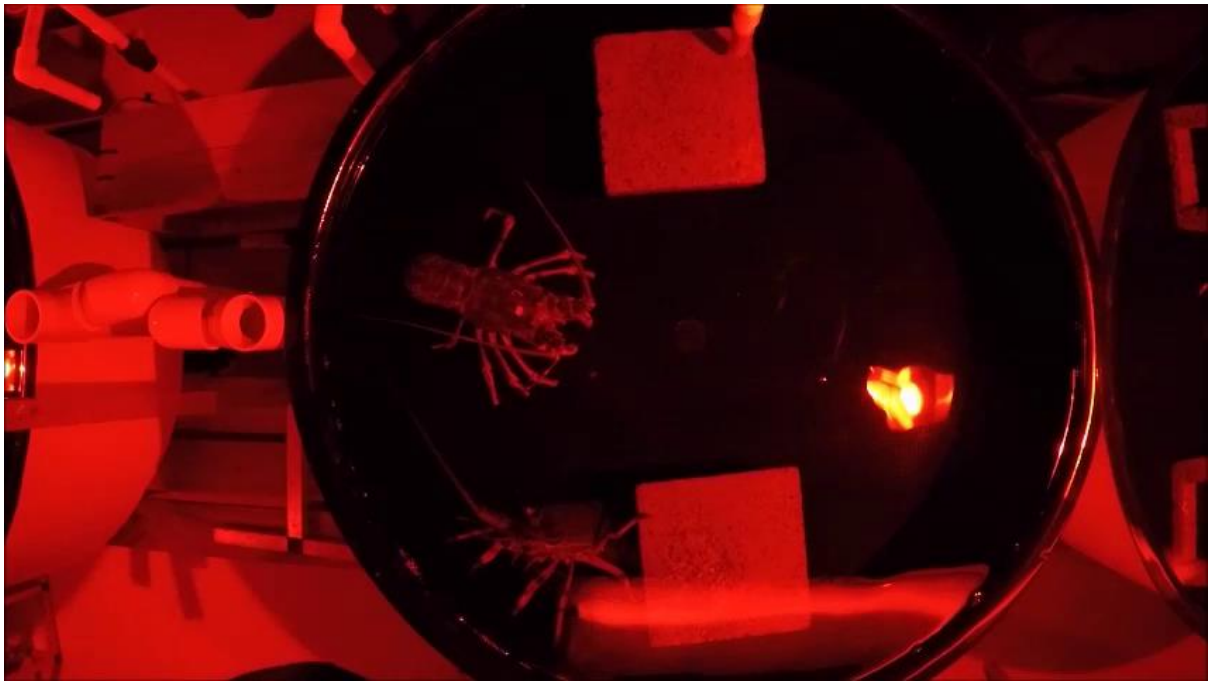

Figure 4.2. Photograph of the lobster competition trial arena.

Video footage of the competitive interactions were analysed for different behaviours including who 'won' the interaction (secured and ate the mussel), handling time of the food item (once the mussel was secured to when it was finished being eaten and the empty shell discarded) and the number of aggressive and submissive behaviours exhibited by the pair of competitors and the level of activity exhibited by both individuals (see Table 4.1 for descriptions). Activity level was scored from 0-3, where scoring was determined by how much movement each lobster exhibited, as defined in Table 4.1.

Table 4.1. Descriptions of the winner of the trials, the aggressive and submissive behaviours exhibited by lobsters during competition trials, and description of level of activity scoring. Descriptions of aggressive and submissive behaviours are adapted from Carter et al. (2014) and Briones-Fourzán et al. (2015). Aggressive and submissive behaviours were scored as a rate of number of events per individual per hour.

Behaviour	**Description**
Winner	The lobster that reached the food first and consumed it, or the lobster that fought for the food, secured possession of it and consumed it. This was recorded at the species that 'won', *Jasus edwardsii* or *Sagmariasus verreauxi*, or as 'neither' if neither species reached and consumed the mussel during the 1 hr trial.
Aggressive behaviours	
Approach	One lobster moves towards the other.
Threat	One lobster flicks antennae or lifts legs in threatening display towards the other.
Physical contact	One lobster physically touches with legs or antennae, grabs or attacks the other.
Submissive behaviours	
Retreat	One lobster moves away from the other in response to the other approaching.
Escape	One lobster utilised a tail flick response to escape the other.
Activity level scoring	
0	No movement by lobster.
1	Lobster active for <10% of the competition period.
2	Lobster active for 10-50% of the competition period.
3	Lobster active for >50% of the competition period.

Data and statistical analysis

All statistical analyses were performed in R (R Core Team 2017). From the 18 pairs of lobsters, a total of 54 successful trials were conducted over the three temperature treatments. Nine trials (three lobster pairs) were excluded due to individuals moulting during or immediately after completion of experiments. Generalised linear mixed models (GLMMs) were used to analyse competition outcomes, using the lme4 package (Bates et al. 2015) and the following model description:

$$\text{Response} = \text{Species} + \text{Temperature} + \text{Species} * \text{Temperature} + (1|\text{Number}) + (1|\text{Pair})$$

This model is used for different responses, where 'response' is the competition outcome winner, the number of aggressive and submissive behaviours, activity level and food handling time. Species and temperature are the predictor variables and the number error term, indicating the 'day number' of food competition trials (the first, second or third day), accounts for the repeated measures aspect of the experiments and the pair error term accounts for each unique size-matched lobster pair. Model covariables (lobster total length, sex and damage) were removed from the model as none showed significance and model fits assessed by Akaike Information Criteria were not improved with their inclusion. The model for assessing the number of wins used a binomial distribution, aggressive and submissive behaviours and activity level used a Poisson distribution and food handling time used a gamma distribution. Where GLMMs were not able to be fitted, Fisher's Exact Test for small sample sizes was used to determine differences.

Results

Jasus edwardsii won significantly more food competition trials than *S. verreauxi* at all temperatures tested (Fisher's Exact Test; p = 0.039, Figure 4.3). There was one instance where the *S. verreauxi* individual reached the food first (at 24 °C) but was then attacked by the *J. edwardsii* who proceeded to secure and consume the mussel. In this case, *J. edwardsii* was considered the winner of the competitive trial.

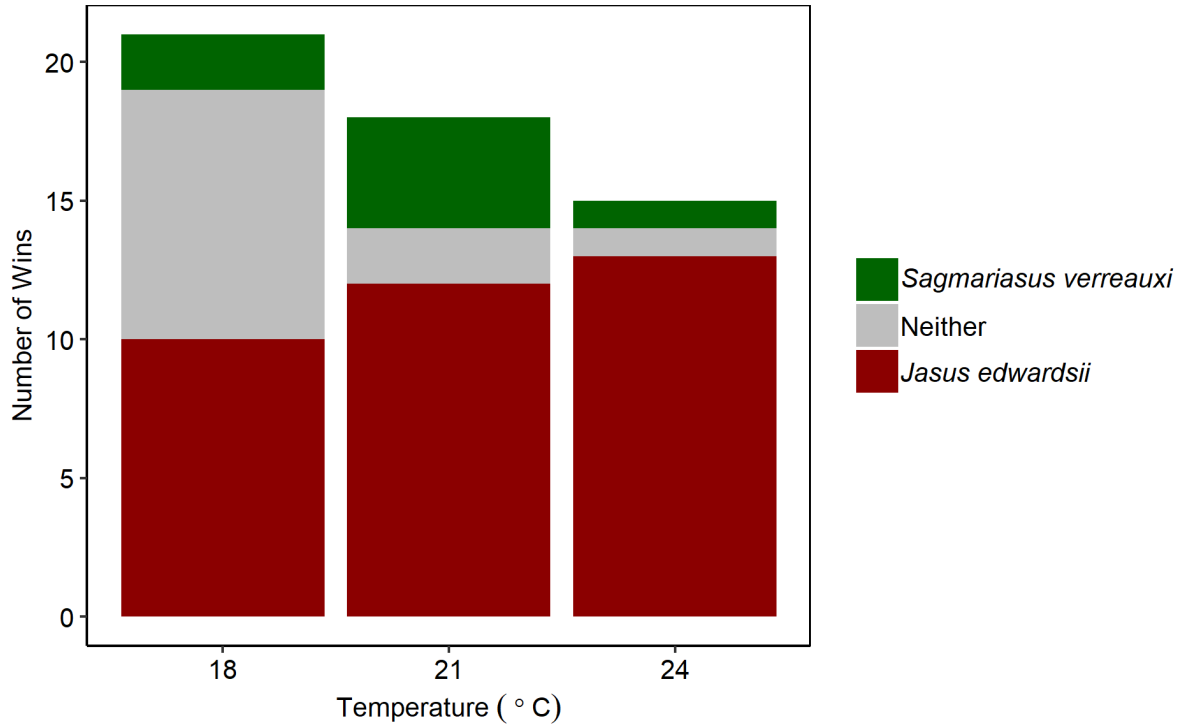

Figure 4.3. The number of food competition wins whereby the lobster secured and ate the mussel by *Sagmariasus verreauxi*, *Jasus edwardsii* or neither where neither lobster secured the mussel in paired competitive feed trials relative to temperature (18°C n = 21 [7 lobster pairs], 21°C n = 18 [6 lobster pairs], 24°C n = 15 [5 lobster pairs]).

The number of aggressive behaviours exhibited was significantly affected by species, where *J. edwardsii* exhibited more aggressive behaviours overall than *S. verreauxi* at all temperatures (GLMM; Species p < 0.001, Table 4.2, Figure 4.4a). Both species showed a trend of being

more aggressive at 21°C however this effect was not statistically significant (GLMM; Temperature p = 0.101, Table 4.2). For submissive behaviours, both species and temperature significantly affected the number of responses, with *S. verreauxi* exhibiting more submissive behaviours than *J. edwardsii* (GLMM; Species p < 0.001, Temperature p = 0.083, Table 4.2, Figure 4.4b). Submissive behaviours increased slightly with temperature for *J. edwardsii*, while the number of submissive responses for *S. verreauxi* at 21 and 24°C were more than twice that compared to 18°C.

Table 4.2. Generalized linear mixed model statistics of the effect of species (*Jasus edwardsii* and *Sagmariasus verreauxi*) and temperature (18, 21 or 24°C) on different behaviours observed during paired competitive food trials. The error term accounts for the repeated measures in the trials (both each trial replicate [1-3] and each lobster pair [1-18]).

	Random effects			**Fixed Effects**				
Model	Factor	Variance	Std. Dev.	Factor	Estimate	Std. Error	z value	Pr (>|z|)
Aggressive	Replicate	0.497	0.705	Species	-2.216	0.520	-4.262	<0.001*
behaviours	Pair	0.111	0.333	Temperature	0.153	0.093	1.642	0.101
Submissive	Replicate	<0.001	<0.001	Species	2.708	0.596	4.542	<0.001*
behaviours	Pair	0.511	0.715	Temperature	0.175	0.101	1.736	0.083
Activity	Replicate	0.007	0.081	Species	-0.656	0.193	-3.405	0.001*
Level	Pair	0.001	0.038	Temperature	0.121	0.038	9.194	0.001*
Handling	Replicate	0.000	0.000	Species	<0.001	0.015	0.000	1
Time	Pair	0.118	0.344	Temperature	0.018	0.016	1.181	0.238

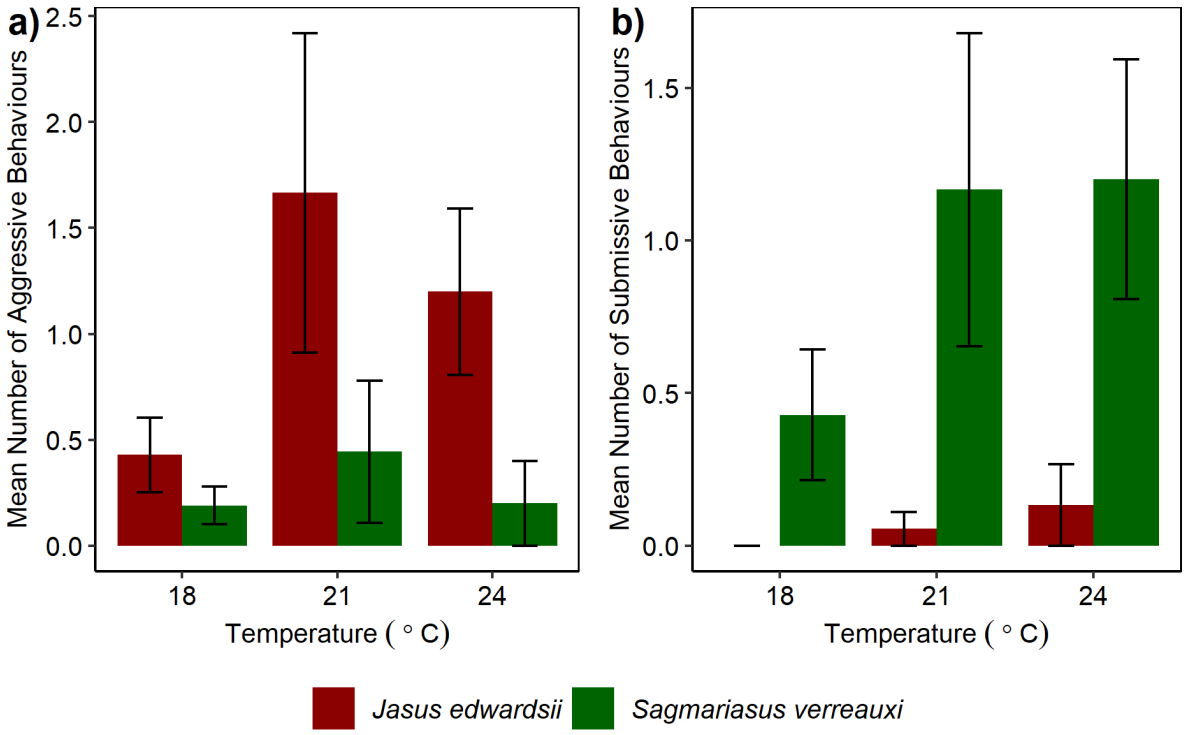

Figure 4.4. The mean ± standard error of the number of a) aggressive and b) submissive behaviours (described in Table 4.1) for *Jasus edwardsii* and *Sagmariasus verreauxi* in competitive feeding trials at 18, 21 and 24°C (n = 21, 18 and 15 respectively).

The rate of different types of behaviours varied among species and temperature treatment. With increasing temperatures, *J. edwardsii* were more likely to approach *S. verreauxi* individuals (Table 4.3). There was also a very high rate of physical contact in the 21°C trials. This was a result of two individuals exhibiting higher levels of aggression than others. This coincided with a high number of retreats and escapes exhibited by *S. verreauxi* at 21°C whereby they were more likely to retreat over actively escaping using tail flick responses (Table 4.2).

Table 4.3. The number of aggressive and submissive behaviours (as described in Table 4.1) exhibited by *Jasus edwardsii* and *Sagmariasus verreauxi* in competitive feeding trials at 18, 21 and 24°C (n = 21, 18 and 15 respectively), by behavioural type.

	Jasus edwardsii			***Sagmariasus verreauxi***		
Behaviour	18°C	21°C	24°C	18°C	21°C	24°C
Aggressive						
Approach	0.14	0.22	0.533	0.05	0.06	0.07
Threat	0.14	0.44	0.27	0.05	0	0
Physical contact	0.19	0.83	0.27	0	0	0.13
Total Aggressive	**0.48**	**1.5**	**1.07**	**0.1**	**0.06**	**0.2**
Submissive						
Retreat	0	0.06	0.07	0.3	0.83	0.87
Escape	0	0	0.07	0.05	0.33	0.13
Total Submissive	**0**	**0.06**	**0.13**	**0.43**	**1.17**	**1**

The level of activity exhibited was significantly affected by both species and temperature (GLMM; Species p = 0.001, Temperature p = 0.001, Table 4.2, Figure 4.5a). *Jasus edwardsii* were more active than *S. verreauxi* during all temperature trials, while during more than half of the trials, the *S. verreauxi* individuals did not move for the one hour filmed period (Figure 4.5a). Food handling time did not vary with species or temperature (GLMM; Species p = 1.000, Temperature p = 0.238, Figure 4.5b).

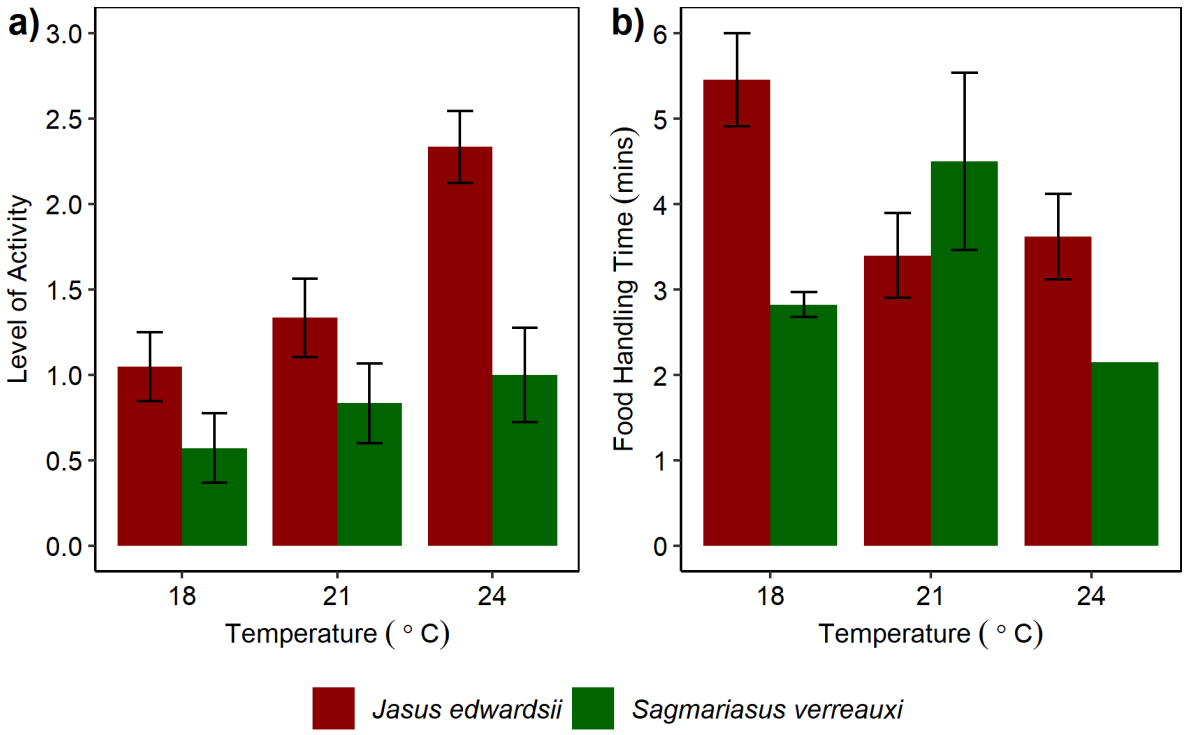

Figure 4.5. The mean ± standard error of a) activity level (from 0-3 behavioural score) and b) food handling time (described in Table 4.1) for *Jasus edwardsii* and *Sagmariasus verreauxi* in competitive feeding trials at 18, 21 and 24°C (Level of activity; n = 21, 18 and 15 respectively, Food handling time; n = 12, 16 and 14 respectively).

Discussion

Here, it was demonstrated that *J. edwardsii* is the dominant competitor when in competition for food with *S. verreauxi* across the full range of temperatures examined (18-24°C). *Jasus edwardsii* exhibited significantly more aggressive behaviours and won more paired competitive feed trials independent of temperature treatment. This is in contrast with behaviours exhibited by *S. verreauxi* that were significantly more submissive. These results indicate that the *J. edwardsii* population in Tasmania may be less vulnerable to dominant interactions and direct food competition resulting from the range extension and increase in abundance of *S. verreauxi*. A previous study on Gulf of Mexico red snapper (*Lutjanus campechanus*) found that this local species exhibited aggressive behaviour in the presence of

range-shifting species and were able to outcompete the new species (Marshak & Heck 2017). This result along with the findings of this study suggest that further range extension of *S. verreauxi* may be contested in areas currently dominated by *J. edwardsii*, potentially slowing the current range extension of *S. verreauxi* with ongoing warming.

Competiveness beyond physiological optima

Interestingly, and in contrast to the original hypothesis it was found that the competitive dominance of *J. edwardsii* sustains beyond its optimal physiological performance. In juvenile *J. edwardsii*, thermal optimum for aerobic scope is ~20°C, followed by declining aerobic performance (Twiname et al. in prep). Other temperature dependent physiological performance indicators, such as optimal growth and feed conversion ratios peak at 20.6°C and 19.3°C respectively in post-pueruli *J. edwardsii* (Thomas et al. 2000). Given that *J. edwardsii* continues to be the dominant competitor up to 24°C, these physiological performance indicators do not necessarily successfully predict competitive outcomes. This continued competitive ability may indicate increased motivation to feed to match increased in metabolic costs at higher temperatures. This was confirmed for juvenile *S. verreauxi*, which showed parallel increases in feed consumption and metabolic rates with increasing temperatures (Fitzgibbon et al., 2017). However, the lack of *S. verreauxi* to become more competitive with increasing temperatures as well, may be explained by a combination of a generally more submissive or inactive behavioural phenotype and lower metabolic demand relative to *J. edwardsii* at identical temperatures (Oellermann et al. in prep).

Aggressive behaviour

Jasus edwardsii won significantly more of the food competition trials than *S. verreauxi*. As the number of aggressive behaviours exhibited by *J. edwardsii* was significantly higher than *S. verreauxi*, it could be assumed that aggression was a key factor in these competitive interactions for food between spiny lobsters. Aggression is considered a key factor in the

successful outcomes of competitive interactions within and between species, where aggressive individuals are more commonly the winner of a resource (Kaiser et al. 1998, Tran et al. 2014). Aggressive behaviour exhibited by *J. edwardsii* here could be linked to higher energetic requirements, where increased food intake is needed to alleviate increased energy requirements with temperature (Fitzgibbon et al. 2017). Thomas et al. (2003) also observed that food restrictions increased intraspecific dominance in *J. edwardsii*. Since both species were fed and starved at the same rate, this indicates that *J. edwardsii* may require more food than *S. verreauxi* at identical temperatures to maintain their metabolic rates. For *J. edwardsii*, increasing energetic cost of higher activity linked to aggression may pay off in increasing success of attaining food resources. Another factor that impacts aggression crustaceans is the presence of berried females. Studies on American lobster (*Homarus americanus*) showed increased aggression in berried females towards other males and non-berried females, influencing their competitive strength (Campbell 1990, Mello et al. 1999).

Submissive behaviour

Sagmariasus verreauxi exhibited significantly lower activity rates and significantly higher numbers of submissive behaviours than *J. edwardsii*, corresponding with fewer food competition wins. Low activity rates were the result of many individuals not moving for the entire trial, instead remaining in or along the side of the shelters. This behaviour could be due to temperature having a negative effect on the species (Seth et al. 2013), as a behavioural mechanism to seek out cooler areas (Gherardi et al. 2013), or as a protective response in lobsters to other predators (Briceño et al. 2018). This indicates that the need for shelter outweighed the need to feed for *S. verreauxi* during the trial conditions. Lack of activity and subsequent lack of 'wins' of the food resource could also be reflective of a lack of motivation to pursue a competitive interaction for food. As temperatures tested were at or below those deemed optimal for *S. verreauxi* (Fitzgibbon et al. 2017, Twiname et al. in prep, Twiname et al. in review), the

challenge to consume sufficient food to meet increased metabolic rates may not be as critical as they are for *J. edwardsii* or indicate lower metabolic demand at identical temperatures. It is likely that the lack of activity and high number of submissive behaviours is due to a combination of factors including conserving energy, low metabolic activity, lack of motivation and potentially fear of attack from the significantly more aggressive *J. edwardsii*.

Limitations

The following limitations apply to this study. Firstly, due to the timing of the experiments, approximately half of the *J. edwardsii* females were berried (6 of 10). While this potentially provided one insight into an aspect of competition between the species, investigating competitive ability when females are not berried would allow for comparisons to be made. Further investigations are required to study the impact of mating, brooding, spawning and moulting on competitive strength. Due to different growth rates and size at maturity between *J. edwardsii* and *S. verreauxi*, matched size pairs of lobsters were of different ages and not at the same stage of sexual maturity. *Jasus edwardsii* reach smaller overall sizes and have smaller sizes at onset of sexual maturity than *S. verreauxi*, resulting in older, sexually mature *J. edwardsii* interacting with similar size but younger and not yet sexually mature *S. verreauxi* in this study (Montgomery 1992, Gardner et al. 2006). There were no trials investigating behaviour of food acquisition when individuals were not in competition. Therefore, it is unknown whether either species becomes aggressive when in contact with a heterospecific individual compared to alone or with a conspecific. The inclusion of an intraspecific and single individual experimental trials would aid in better investigating specific drivers of competitive ability. Individual size has also been determined as a factor in the aggression and outcome of competitive interactions in crustaceans (Thomas et al. 2003). As matched size pairs of lobsters were used in this study, we cannot comment on the outcome of interactions between difference sized individuals that would likely occur in the wild. Exploring the effect of smaller versus

larger individuals of both species would also further our understanding of the competitive interaction between these species.

Future research

Future research directions could include competition under conditions stated above in terms of different size, sex and reproductive stage pairs of lobsters. An interesting behaviour observed by local divers in Tasmania is that *S. verreauxi* appear to form dens where many individuals of different sizes live together in a small area (Redmap sighting number 522, Redmap Australia (2018)) This is different to *J. edwardsii* that have not been recorded exhibiting such behaviour. The effect of this behaviour could be investigated using multiple lobsters in competitive trials to see if the highly gregarious behaviour of *S. verreauxi* could be a 'safety in numbers' strategy. Another is the strength of competition for other resources such as shelter or habitat. One striking result of these experiments was the general lack of activity exhibited by *S. verreauxi*. This species was more likely to remain in a shelter than be active or even non-active but out in the open. Potentially contrasting results for different competitive interactions may suggest different stressors on the two species that could be explored and potentially explained by other performance measures (Twiname et al. in prep). It is likely that the extension of *S. verreauxi* further into Tasmanian waters is facilitated by the increase in the strength and extent of the East Australian Current, as well as warming ocean temperatures allowing over-winter survival of new recruits (Booth et al. 2007, Ridgway 2007, Cetina-Heredia et al. 2015). Previous studies have found differences in the performance measures of lobsters including differences among life stages (Twiname et al. in prep). This suggests that the competitive ability of *J. edwardsii* and *S. verreauxi* may change depending on their life stage and the specific environmental pressures they may be experiencing. Investigating the competitive ability of puerulus and juveniles stage lobsters would provide a more robust insight to competitive dynamics and potential outcomes now and in the future under a changing climate.

Conclusion

In conclusion, it was found that *J. edwardsii* is the dominant competitor for food in laboratory trials. This finding has implications for the continued extension and increase in abundance of *S. verreauxi* in Tasmania as it appears that *J. edwardsii* could potentially be resilient to direct competition for food resources with the expansion of this range-shifting species. If *S. verreauxi* are negatively affected by increases in temperature at the northern, equatorward edge of their range (Fitzgibbon et al. 2014), and restricted at the southern, polewards edge by aggressive, competitively advantaged *J. edwardsii*, *S. verreauxi* may end up with a compressed geographical distribution. Future research should look to determining the competitive ability for different resources and between different sizes, sexes, numbers and life stages of both lobster species.

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CHAPTER 5

Physiology and competitive interactions influence modelled outcomes of climate change on a resident and a range-shifting species.

Abstract

Species redistributions are one of the most commonly documented changes in our oceans as a result of climate change and are occurring globally. To date, many models trying to predict these 'range shifts' of species have used a correlative approach. While correlative models are informative and useful, it has been suggested that these models may not consider important mechanisms that drive species range shifts. Models of Intermediate Complexity for Ecosystem assessments (MICE) are focused, flexible models that can incorporate a variety of data allowing them to become more mechanistic in nature than purely correlative models. Here, a MICE is developed that incorporates data on physiology, competition and population dynamics to project changes in biomass and distribution of a local and non-local range-shifting species of spiny lobster in Tasmania, Australia. Model results of projected biomass suggest that the range-shifting species increases in Tasmanian waters under future ocean warming scenarios, and that this is driven in part by the physiological effect on new recruits into the region. The model suggests that physiological effects have little impact on the local lobster species abundance in response to environmental change, however also suggests that competitive interactions with the range-shifting species will result in decreases in local species projected biomass in some areas. This result is modified by projected heatwave simulations, where increased temperatures beyond ocean warming positively influenced both species. This study demonstrates how physiological data can be integrated in MICE and emphasises that physiological parameters can greatly affect the outcome of model projections.

Keywords: *aerobic scope, climate change, escape speed,* Jasus edwardsii, *MICE, physiology, redistribution, spiny lobster,* Sagmariasus verreauxi, *thermal tolerance*.

Introduction

Climate change is causing widespread alterations to marine ecosystems globally (Hoegh-Guldberg & Bruno 2010, Pecl et al. 2017). One of the most prevalent and pervasive effects observed to date has been the redistribution of species in response to the changing climate (Poloczanska et al. 2013). These 'range shifts' have the potential to alter marine ecosystem structure and function. Greater understanding and the ability to project potential changes in species geographical ranges as a result of ocean warming will allow us to better inform management and conservation of species, supporting us to adapt and mitigate to changes in our oceans.

In the south-east of Australia, ocean warming is occurring up to four times faster than the global average (Hobday & Pecl 2014, Pecl et al. 2014). This accelerated change in the physical environment has already led to many biological changes in the system, including the range extensions of many species poleward along the coast (Pitt et al. 2010, Last et al. 2011, Sunday et al. 2015). One of these species is the eastern rock lobster, *Sagmariasus verreauxi*, a large species of spiny lobster most commonly found along the coast of New South Wales, which has been observed more frequently in Tasmanian waters in recent years (Robinson et al. 2015). This species has been identified as a species likely having undergone a range shift into Tasmania via the extension of the East Australian Current that is transporting warmer water further south, bringing with it tropical and sub-tropical larvae (Ridgway 2007, Robinson et al. 2015). This species is now likely coming into contact with the local species in the area, the southern rock lobster, *Jasus edwardsii*. Previous studies have examined the thermal tolerances of the two species and found that *S. verreauxi* has the thermal capacity to expand its range further into Tasmanian waters and increase its abundance with future ocean warming (Twiname et al. in review).

Models of intermediate complexity for ecosystem assessments (MICE) are tactical, flexible models that allow for the incorporation of a variety of different data types while restricting the focus of the model to specific questions (Plagányi et al. 2014). Their ability to incorporate an 'intermediate' amount of information provides a platform between the complex end-to-end full ecosystem models and simple single-species assessment models, making them more accessible as well as providing more targeted advice (Plagányi et al. 2014, Collie et al. 2016). MICE can be used to examine selected parts of an ecosystem, are able to account for uncertainties in chosen parameters and can evaluate model performance (Plagányi et al. 2014). Here, a MICE was used to investigate the possible outcomes of a new interaction between a range-shifting species (*S. verreauxi*) and a local species (*J. edwardsii*) of lobster in a fast-warming ocean region off the south-east coast of Australia, focusing on the Tasmanian east coast. In this study, a novel extension to MICE by integrating physiological and competitive interaction data to account for potential changes in lobster performance under ocean warming scenarios is presented.

The aim of this study was to develop a MICE to project changes in biomass of both species of lobster in four spatial zones off the east coast of Tasmania, under future ocean warming and heatwave scenarios. Due to the nature of implementing a two-part model (incorporating physiological parameters [part one] and then competitive interactions [part two]), there are two opposing hypotheses; (i) based on thermal tolerance data alone, *S. verreauxi* will be projected to increase in biomass in Tasmania in future scenarios and (ii) as a consequence of positive effects of warming on competitive ability, the local species will outcompete the range-expanding species.

Methods

Modelling approach

A MICE was developed using an age-structured framework for two species of lobster to model the dynamics of a resident and a range-shifting species along the east coast of Tasmania. Consistent with the philosophy of starting simple and adding complexity in a stepwise fashion, the model focuses on the two species of lobster only (no predator or prey species) and two alternative model versions are developed. Model 1 includes physiological data of thermal tolerances to determine how each species will be affected by future ocean warming scenarios and assumes environmental but not interspecific competitive influences. Model 2 is an extension of Model 1 where complexity is added to account for competitive interactions represented via a joint carrying capacity and competitive interaction for both species. The model was coded in AD Model Builder™ (Fournier et al. 2012), fitted to available fisheries data and sensitivity analyses were conducted to examine parameter and model structural uncertainty.

Model species

Southern rock lobster, *Jasus edwardsii*, is the local lobster species found in Tasmania. It is one of the most valuable fisheries in Tasmania, as well as being important ecologically and socially (Pecl et al. 2009). Eastern rock lobster, *Sagmariasus verreauxi*, is a large species of lobster usually found along the eastern coast of Australia and historically in northern Tasmania (Figure 5.1, zone 4) but is suspected of undergoing a range shift further into Tasmanian waters in recent years (Robinson et al. 2015). This species, while also an important fished species, is less valuable than the local *J. edwardsii*, and it is currently unknown how this species may interact with the local species of lobster in Tasmania.

Spatial structure

The model is spatially structured over four areas along the east coast of Tasmania, coinciding with existing rock lobster fishing zones (Figure 5.1, zones 1-4, Green et al. (2011)). In the model it is assumed that there is no movement of the adult or newly recruited lobsters between the different zones but assume that the recruits are introduced to the zones via the East Australian Current. Due to significant differences in the stock sex ratios and growth parameters of *J. edwardsii* between the different zones, appropriate sex-specific and zone-specific parameters were used for each of these from the literature (Gardner and van Putten 2008, Montgomery et al. 2009).

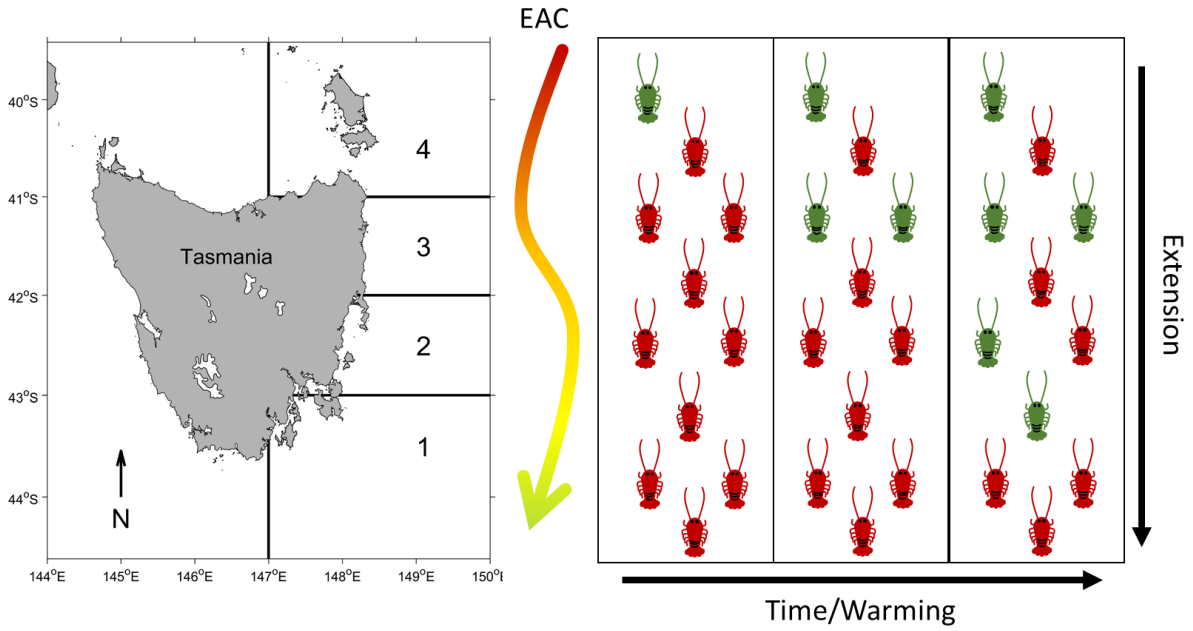

Figure 5.1. Map of Tasmania including the four spatial areas in the model coinciding with commercial rock lobster fishing zones 1-4 along the east coast, and schematic of the hypothesised changes in range and abundance of *Sagmariasus verreauxi* (green lobsters) and *Jasus edwardsii* (red lobsters) with time and ocean warming in the region due to increased transport of warmer water south by the East Australian Current (EAC).

Data input

Historical catch per unit effort (CPUE) data from the Tasmanian southern rock lobster fishery (*J. edwardsii*) were obtained from the Institute for Marine and Antarctic Studies (IMAS) for the period 1970-2017. As there is no formal fishery for *S. verreauxi* in Tasmania, the model was seeded with recorded sightings of *S. verreauxi* in Tasmania from IMAS rock lobster surveys and observational data of first sightings of puerulus (recruiting lobsters, IMAS, unpublished data) as well as sightings of adults along the east coast of Tasmania from citizen science observations (Redmap Australia 2017). Here, the first puerulus sighting in the northern zones (zone 3) was observed in 1997, and the first puerulus sighting in the south (zone 1) was observed in 2010 (IMAS, unpublished data). The first adult *S. verreauxi* recorded in Tasmania by IMAS was in 2004 (IMAS, unpublished data), however, adult *S. verreauxi* have been very occasionally anecdotally reported in Tasmania by recreational and commercial fishers for several decades.

Jasus edwardsii population data varied greatly among the different spatial zones, including for stock sex ratios, von Bertalanffy growth parameters and fishing size selectivity (Gardner & Van Putten 2008). Based on these differences, *J. edwardsii* data were disaggregated by sex for the four zones and different parameters were used for each zone. As growth and size data for *S. verreauxi* was similar for both males and females (Montgomery et al. 2009), all estimates of projected biomass are for combined males and females in the population.

Model 1: Lobster age-structured model

Model 1 is built in a stepwise fashion and then modified to simulate different scenarios by adjusting parameters and model structure based on Model 1A (see Tables 5.1 and 5.2). Model 1A is the 'base' model scenario. Here, two species of lobster, *J. edwardsii* and *S. verreauxi*, are used. Herein, abbreviations of the species common names of SRL (southern rock lobster) are used for *J. edwardsii* parameters and ERL (eastern rock lobster) for *S. verreauxi* parameters.

Puerulus recruitment is modelled assuming external recruitment for *S. verreauxi* and self-recruitment for *J. edwardsii*. External recruitment of *S. verreauxi* is a fixed number recruiting into the four spatial zones following a gradient of higher puerulus recruitment in the north and less in the south based on thermal tolerance assumptions (Twiname et al. in prep-b, in review). The model uses the Beverton-Holt stock recruitment relationship and assumes recruitment is local to each of the spatial zones i.e. there is no sharing between the zones. As we do not know if there is sharing between the zones, this lessens the complicated nature of the model. The stock sex ratio for *S. verreauxi* is assumed to be 50:50 due to lack of catch data in Tasmania, but for *J. edwardsii* the stock sex ratio is 40:60 males to females (Gardner et al. 2003). This, however, is opposite to the *J. edwardsii* commercial catch sex ratio of 60:40 males to females (C. Gardner, pers. comm.). This skewed catch sex ratio was accounted for in the model by including this assumption as a catch sex proportion factor for *J. edwardsii* (*qf*; Table 5.3).

Von Bertalanffy growth equations were used to model the somatic growth of both lobster species. There is no growth information available for *S. verreauxi* in Tasmania and so parameters were used from the population in New South Wales, north of the study area (Montgomery et al. 2009). Age at maturity is estimated using size at maturity data and growth calculations and is applied in the model as a knife edge value (Table 5.3). Once a lobster reaches 10 years in the model, it is assigned to a 'plus group'. Population growth is calculated as the increase in projected biomass via recruitment into the local population minus natural mortality and fishing catches (Table 5.1, Equations 1-5). Model 1A assumes population growth of *S. verreauxi* is driven by external input of puerulus. *Jasus edwardsii* is assumed to have self-recruitment only. The model also assumes no movement of adults between zones via walking or migrating.

For Model 1, carrying capacities, K, for *J. edwardsii* K(SRL), and *S. verreauxi* K(ERL), are estimated separately for each spatial zone. Carrying capacity K(SRL) for *J. edwardsii* is

estimated by fitting the model to historical CPUE data. As no data are available to be able to accurately estimate carrying capacity K(ERL) for *S. verreauxi*, it is set at a low fixed value, and hence model trajectories show relative change rather than absolute values.

Physiological data to be incorporated in the model were sourced from Twiname et al. (in prep-b). These data included aerobic scope and escape speed thermal performance equations. Aerobic scope is a valuable physiological measure that has been widely explored, with support for and against its use as a predictor for species performance under climate change (Pörtner & Knust 2007, Pörtner & Farrell 2008, Clark et al. 2013, Jutfelt et al. 2018). However, as a single measure of performance it does not necessarily predict whole-organism performance (Norin et al. 2014, Fitzgibbon et al. 2017, Twiname et al. in prep-b, in review) and is therefore combined with escape speed thermal tolerances to provide a more robust physiological multiplier for survival. These physiological performance measures were input as quadratic equations with performance as a function of temperature (Table 5.1, Equations 13-16). Values for these equations are supplied as physiological constants (c^s), are numerically labelled (1-12) as each value is unique and corresponds to a certain equation and are supplied in Table 5.4. The physiological factors were applied (as the outcome of the quadratic equations 13-16, Table 5.1) as inverses to the natural mortality estimate *M*, such that increases in performance resulted in decreased mortality (Table 5.1, Equations 2-5). The model is projected forward at monthly time steps (to 2050) using sea surface temperature projections available from 2006. Sea surface temperature (SST) for the future period were provided by the CSIRO Ocean Downscaling Project. A global high-resolution ocean general circulation model is used to dynamically downscale climate changes in the 21st century derived from Coupled Model Intercomparison Project Phase 5 (CMIP5) climate models (R. Matear).

Table 5.1. Model 1 equations, where 'SRL' indicates *Jasus edwardsii* and 'ERL' indicates *Sagmariasus verreauxi*. Parameters in equations are further defined in Table 5.2. Here, *s* denotes the species identifier where *s* = 1 are *J. edwardsii* females, *s* = 2 are *J. edwardsii* males and *s* = 3 are combined female and male *S. verreauxi*.

Model description	**Equations**	**No.**
Recruitment	$N^{s}_{z,y+1,1,1} = qf^{s}_{z} \times R^{s}_{z,y+1} \times PA^{s}_{z,y,t} \times PE^{s}_{z,y,t} \quad s \le 2$ $N^{3}_{z,y+1,1,1} = R^{3}_{z,y+1} \times PA^{3}_{z,y,t} \times PE^{3}_{z,y,t} + \varphi^{3}_{z,y,t} \quad s = 3$ Where $s \le 2$ represents SRL, and $s = 3$ represents ERL	1
Update population during each month of the year	$N^{s}_{z,y,a,t+1} = N^{s}_{z,y,a,t}\, e^{-M^{s} \big/ A^{s}_{z,y,t} \times E^{s}_{z,y,t}} - C^{s}_{z,y,a,t}$ For $a<m$ and $t<12$	2
Update the plus group population size during each month of the year	$N^{s}_{z,y,m,t+1} = N^{s}_{z,y,m,t}\, e^{-M^{s} \big/ A^{s}_{z,y,t} \times E^{s}_{z,y,t}} - C^{s}_{z,y,m,t}$ For $a=m$ and $t<12$	3
Update population from one year to the next	$N^{s}_{z,y+1,a+1,1} = N^{s}_{z,y,a,12}\, e^{-M^{s} \big/ A^{s}_{z,y,12} \times E^{s}_{z,y,12}} - C^{s}_{z,y,a,12}$ For $a<m$ and $t=12$	4
Update the plus group from one year to the next	$N^{s}_{z,y+1,m,1} = N^{s}_{z,y,m,12}\, e^{-M^{s} \big/ A^{s}_{z,y,12} \times E^{s}_{z,y,12}} - C^{s}_{z,y,m,12} + N^{s}_{z,y,m-1,12}\, e^{-M^{s} \big/ A^{s}_{z,y,12} \times E^{s}_{z,y,12}} - C^{s}_{z,y,m-1,12}$ For $a=m$ and $t=12$	5
Beverton-Holt stock-recruitment relationship	$R^{s}_{z,y} = \dfrac{\alpha^{s}_{z} B^{sp,s}_{z,y-1}}{\beta^{s}_{z} + B^{sp,s}_{z,y-1}}$	6
Spawning biomass of species *s* in zone *z* at the start of year *y*¶	$B^{sp,s}_{z,y} = \sum_{a=1}^{z} f^{s}_{a} w^{s}_{a} N^{s}_{z,y,a,t}$	7
	$\beta^{s}_{z} = \dfrac{\left(K^{sp,s}_{z}\right)\left(1 - 5h^{s} 0.2\right)}{5h^{s} - 1}$	8
	$\alpha^{s}_{z} = \dfrac{\beta^{s}_{z} + \left(K^{sp,s}_{z}\right)}{SPR^{s}_{virg}}$	9
	$SPR^{s}_{virg} = \sum_{a=1}^{z} f^{s}_{z,a} w^{s}_{z,a,t} N^{virg,s}_{z,a}$	10
	$N^{virg,s}_{z,1} = 1$	11
	$N^{virg,s}_{z,a} = N^{virg,s}_{z,a-1} e^{-M^{s}}$ for $2 < a \le m$	12
Juvenile aerobic scope multiplier	$A^{s}_{z,y,t} = \left(c^{s}_{1} \times \left(T_{z,y,t}\right)^{2} + c^{s}_{2} \times T_{z,y,t} + c^{s}_{3}\right) \Big/ A^{s}_{base}$	13
Juvenile escape speed multiplier	$E^{s}_{z,y,t} = \left(c^{s}_{4} \times \left(T_{z,y,t}\right)^{2} + c^{s}_{5} \times T_{z,y,t} + c^{s}_{6}\right) \Big/ E^{s}_{base}$	14
Puerulus aerobic scope multiplier	$PA^{s}_{z,y,t} = \left(c^{s}_{7} \times \left(T_{z,y,t}\right)^{2} + c^{s}_{8} \times T_{z,y,t} + c^{s}_{9}\right) \Big/ PA^{s}_{base}$	15

Puerulus escape speed multiplier	$PE^s_{z,y,t} = \left(c^s_{10} \times \left(T_{z,y,t}\right)^2 + c^s_{11} \times T_{z,y,t} + c^s_{12}\right) \Big/ PE^s_{base}$	16
Catch by mass in year *y*	$C^s_{z,y,a,t} = w^s_{z,y,a,t} N^s_{z,y,a,t} e^{-M^s} S^s_{z,a} F^s_{z,y,a,t}$	17
Exploitable biomass	$B^{exp,s}_{z,y,t} = \sum_{a=1}^{m} w^s_{z,a,t} S^s_{z,a} N^s_{z,y,a,t}$	18
Proportion of each species harvested	$F^s_{z,y,t} = C^{tot,s}_{z,y,t} / \left(B^{exp,1}_{z,y,t} + B^{exp,2}_{z,y,t}\right)$	19
Numbers-at-age removed each year by age class	$C^s_{z,y,a,t} = S_{z,a} F^s_{z,y,t} N^s_{z,y,a,t}$	20
Fishing	$1 - F = e^{-F^*}$	21
Pre-exploitation biomass	$B^s_{z,0} = K^s_z$	22
Starting age structure	$N_{y_0,a} = R_{start} N_{start,a}$ for $1 \le a \le m$	23
	$N_{start,1} = 1$	24
	$N_{start,a} = N_{start,a-1} e^{-M_{a-1}}$ for $2 \le a \le m-1$	25
von Bertalanffy growth curve	$L_t = L_\infty (1 - e^{-\kappa(t-t_0)})$	26
Weight length relationship	$w^s_{z,y,a,t} = p_1 \times L^{p_2}_t$	27
Log-likelihood	$I^i_{z,y} = \hat{I}^i_{z,y} \exp\left(\varepsilon^i_{z,y}\right) \quad or \ \varepsilon^i_{z,y} = \ell n\left(I^i_{z,y}\right) - \ell n\left(\hat{I}^i_{z,y}\right)$	28
Corresponding model estimate	$\hat{I}^i_{z,y} = q^i \hat{B}^{exp,SRL}_{z,y,t}$	29
Negative log-likelihood	$-\ell nL^{CPUE} = \sum_i \sum_z \sum_y \left[\ell n\left(\sigma^i\right) + \left(\varepsilon^i_{z,y}\right)^2 / 2\left(\sigma^i\right)^2 \right]$	30
Maximum likelihood value	$\hat{\sigma}^i = \sqrt{1 \Big/ n_{i,z} \sum_z \sum_y \left(\ln I^i_{z,y} - \ln \hat{I}^i_{z,y}\right)^2}$	31
Catchability coefficient	$\ell n\, \hat{q}^i = 1 \Big/ n_{i,z} \sum_z \sum_y \left(\ln I^i_{z,y} - \ln \hat{B}^{ex,SRL}_{z,y,t}\right)$	32

¶The 'virg' term in Equations 9-12 refers to virgin biomass which is the estimated pre-exploitation biomass of the species.

Table 5.2. Model 1 variable and parameter definitions.

Variable/ Parameter	Description	Input/ Computed/ Estimated
$N^{s}_{z,y,a,t}$	Number of lobsters of species or sex *s* in zone *z* of age *a* in month *t* of year *y*	Computed from equations 1-5
$R^{s}_{z,y+1}$	Recruitment (number of 1-year-old lobsters) of species *s* in zone *z* at the start of year *y*	Computed from equation 6
$\varphi^{s}_{z,y+1}$	Immigration (number of 1-year-old lobsters) of recruits of species *s* in zone *z* at the start of year *y*	Input, Table 5.3
qf^{s}_{z}	Proportion of the recruits of each sex *s* of SRL in zone *z*	Input, Table 5.3
M^{s}	Monthly natural mortality rate on lobsters of species/sex *s*	Input, Table 5.3
$C^{s}_{z,y,a,t}$	Predicted number of lobsters of species *s* in zone *z* of age *a* caught in month *t* of year *y*	Computed from equation 19
$A^{s}_{z,y,t}$	Aerobic scope survival multiplier for juveniles for species *s* in zone z and month *t* of year *y*	Computed from equation 13
$E^{s}_{z,y,t}$	Escape speed survival multiplier for juveniles for species *s* in zone z and month *t* of year *y*	Computed from equation 14
$PA^{s}_{z,y,t}$	Aerobic scope survival multiplier for puerulus for species *s* in zone z and month *t* of year *y*	Computed from equation 15
$PE^{s}_{z,y,t}$	Escape speed survival multiplier for puerulus for species *s* in zone z and month *t* of year *y*	Computed from equation 16
m	Maximum age considered (taken to be 10), before being added to the plus group	Estimated
$\alpha^{s}_{z}, \beta^{s}_{z}$	are spawning biomass-recruitment relationship parameters for species *s* in zone *z*	Computed from equations 8 & 9
$B^{sp,s}_{z,y}$	Spawning biomass of species *s* in zone *z* at the start of year *y*	Computed from equation 7
f^{s}_{a}	Proportion of lobsters of species *s* of age *a* that are mature	Input, Table 5.3
$K^{sp,s}_{z}$	Pre-exploitation equilibrium spawning biomass (tonnes)	Estimated or fixed
h^{s}	Steepness of stock recruitment relationship for species *s*	Input
$T_{z,y,t}$	Projected sea surface temperature in zone *z* and month *t* of year *y*	Input
c^{s}_{1}	Juvenile aerobic scope constant for species *s*	Input, Table 5.4
c^{s}_{2}	Juvenile aerobic scope constant for species *s*	Input, Table 5.4
c^{s}_{3}	Juvenile aerobic scope constant for species *s*	Input, Table 5.4
A^{s}_{base}	Constant multiplier for juveniles for species *s* to base year 2006	Input, Table 5.4
c^{s}_{4}	Juvenile escape speed constant for species *s*	Input, Table 5.4
c^{s}_{5}	Juvenile escape speed constant for species *s*	Input, Table 5.4
c^{s}_{6}	Juvenile escape speed constant for species *s*	Input, Table 5.4
E^{s}_{base}	Constant multiplier for juveniles for species *s* to base year 2006	Input, Table 5.4
c^{s}_{7}	Puerulus aerobic scope constant for species *s*	Input, Table 5.4
c^{s}_{8}	Puerulus aerobic scope constant for species *s*	Input, Table 5.4
c^{s}_{9}	Puerulus aerobic scope constant for species *s*	Input, Table 5.4
PA^{s}_{base}	Constant multiplier for puerulus for species *s* to base year 2006	Input, Table 5.4
c^{s}_{10}	Puerulus escape speed constant for species *s*	Input, Table 5.4

c_{11}^{s}	Puerulus escape speed constant for species *s*	Input, Table 5.4
c_{12}^{s}	Puerulus escape speed constant for species *s*	Input, Table 5.4
PE_{base}^{s}	Constant multiplier for puerulus for species *s* to base year 2006	Input, Table 5.4
L_t	Length at age *t* (mm)	Computed from equation 26
L_∞	Asymptotic maximum length (mm)	Input, Table 5.3
κ	Growth rate coefficient	Input, Table 5.3
t_0	Age at which species has zero length	Input, Table 5.3
$w_{z,y,a,t}^{s}$	Mass of lobsters of species s and age *a* in zone *z* during month *t* of year *y* (tonnes)	Computed from equation 27
p_1	Weight-length parameter 1	Input, Table 5.3
p_2	Weight-length parameter 2	Input, Table 5.3
l	Carapace length in mm	Input
$S_{z,a}^{s}$	Commercial selectivity (i.e. vulnerability to fishing gear) of species s and age *a* in zone *z*	Input, Table 5.3
$F_{z,y,a,t}^{s}$	Fished proportion of a fully selected age class of species s and age *a* in zone during month *t* of year *y*	Computed
$C_{z,y,t}^{tot,s}$	Total catch by mass from zone *z* in year *y* and month *t* (tonnes)	Computed from equation 17
F	Fully selected fishing proportion	Input
F^*	Annual fishing mortality rate	Input
$B_{z,0}^{s}$	Pre-exploitation biomass in tonnes	Estimated
$I_{z,y}^{i}$	CPUE abundance index for year *y*, zone *z* and catch period series *i*	Computed from equation 28
$\hat{B}_{z,y,t}^{exp,SRL}$	Combined male and female exploitable biomass of SRL in zone *z*, year *y* and a catch period *t* in tonnes ¶	Computed from equation 18
q^{i}	Catchability coefficient for the *i*th abundance index	Computed
$\varepsilon_{z,y}^{i}$	From $N\left(0,\left(\sigma^{i}\right)^{2}\right)$	Computed

¶ Catch period *t* references the 8 catch periods in the year that include the 12 months, where catch period 1 is March, 2 is April, 3 is May + June + July, 4 is August + September + October, 5 is November, 6 is December, 7 is January and 8 is February.

Table 5.3. Model 1 fixed parameter settings for *Jasus edwardsii* (SRL, sex separated) and *Sagmariasus verreauxi* (ERL, sexes combined). Square brackets indicate where different values are used for the four spatial zones, defined as [Zone 1]; [Zone 2]; [Zone 3]; [Zone 4].

Parameter	SRL female	SRL male	ERL	Source/Reference
Age at maturity	4	4	4	Montgomery (1992), Gardner et al. (2006)
M^s	$8.33e^{-3}$	$8.33e^{-3}$	$1.5e^{-2}$	Punt and Kennedy (1997), fixed input
$\varphi^s_{z,y+1}$	NA	NA	[400]; [600]; [800]; [1000]	Assumed
L_∞	[112.28]; [112.73]; [127.39]; [147.79]	[122.67]; [122.67]; [178.12]; [184.26]	[239.77]; [239.77]; [239.77]; [239.77]	Gardner and Van Putten (2008), Montgomery et al. (2009)
κ	[0.0978]; [0.0979]; [0.1701]; [0.3029]	[0.3014]; [0.3015]; [0.1390]; [0.2601]	[0.13]; [0.13]; [0.13]; [0.13]	Gardner and Van Putten (2008), Montgomery et al. (2009)
t_0	[0]; [0]; [0]; [0]	[0]; [0]; [0]; [0]	[0]; [0]; [0]; [0]	Gardner and Van Putten (2008), Montgomery et al. (2009)
$S^s_{z,a}$	[10]; [10]; [10]; [4]	[4]; [7]; [8]; [7]	[5]; [5]; [5]; [5]	Calculated from data in Gardner and Van Putten (2008), Montgomery et al. (2009)
qf	0.5	0.5	0.5	Assumed
q^i	0.4	0.6	0.5	C. Gardner, pers. comm. and assumed
p_1	0.000271	0.000285	0.0026	Gardner and Van Putten (2008), Montgomery et al. (2009)
p_2	3.146	3.125	2.76	Gardner and Van Putten (2008), Montgomery et al. (2009)

Table 5.4. Physiological constants for aerobic scope and escape speed multiplier parameters, sourced from Twiname et al. (in prep-b, in review), where SRL indicates *Jasus edwardsii* and ERL indicates *Sagmariasus verreauxi*.

Aerobic scope constants			Escape speed constants		
	SRL	ERL		SRL	ERL
c^s_1	-0.005	-0.004	c^s_4	-0.005	-0.007
c^s_2	0.190	0.209	c^s_5	0.235	0.331
c^s_3	-1.451	-2.032	c^s_6	-0.968	-2.434
A^s_{base}	0.297	0.071	E^s_{base}	1.305	0.858
c^s_7	-0.005	-0.010	c^s_{10}	-0.006	-0.005
c^s_8	0.181	0.531	c^s_{11}	0.232	0.214
c^s_9	-1.139	-5.983	c^s_{12}	-1.387	-1.720
PA^s_{base}	0.501	0.116	PE^s_{base}	0.654	0.392

Model 1 scenarios

Model 1 scenarios are summarised in Table 5.5. To elaborate, all models progress from Model 1A which is considered the 'base' model from which new scenarios are developed. Model 1A incorporates the physiological data applied to the population and recruitment equations (Equation No. 1-5). In this scenario, fishing mortality is set based on the average fishing mortality for the past five years (2012-2017) for the *J. edwardsii* fishery and at zero for *S. verreauxi*.

Model 1B removes the physiological multipliers and hence assumes no effect of projected temperature changes on the physiology during the projection.

Model 1C removes the physiological effects from the recruitment but not adult population equations. This enables comparison of the relative effect of temperature and performance changes operating on the entire population versus assuming no physiological impacts on the recruits.

Model 1D incorporates simulations of marine heatwave events by proportionately increasing the temperature projections via the use of a temperature multiplier. This allowed for temperatures to exceed those predicted in the near future and provide a platform to explore higher temperature effects such as those that may be experienced by a marine heatwave. As marine heatwaves are predicted to occur increasingly in south east Australia (Oliver et al. 2018), it is important to investigate the potential effects these events may have on the system.

Models 1E and 1F simulate effects of changing fishing mortality on *J. edwardsii*, either increases (Model 1E, set at five times the average fishing mortality from Model 1A) or decreases to zero mortality (Model 1F).

Table 5.5. Model 1 scenarios. See Table S5.1 for more details on changes to parameters and model estimates.

Model 1	Description
Model 1A	Physiological multipliers applied to population and recruitment equations, assumes average fishing from the past 5 years
Model 1B	No physiological multipliers applied to any equations
Model 1C	Physiological multipliers applied only to adult population equations, not to the recruitment equations
Model 1D	Model 1A + Heatwave simulation
Model 1E	Model 1A + high fishing mortality
Model 1F	Model 1A + zero fishing mortality

Model 1 fitting and likelihood equations

The model was fitted to the available *J. edwardsii* CPUE abundance indices by maximising the likelihood function. The model equations are given in Table 5.1, and the contributions to the log-likelihood function from the different data subsets are shown in Tables S5.1-S5.4. Quasi-Newton minimization is used to minimize the total negative log-likelihood function. The package AD Model Builder^{TM} (Fournier et al. 2012) is used for this purpose.

Model 1 sensitivity tests

Sensitivities performed on different model parameters are summarised in Table 5.6. The first sensitivity test investigated the effect that different marine heatwave multiplier strengths had on projected biomass. Second, as there is high variation in the age at sexual maturity and growth rates of *J. edwardsii* around Tasmania, different variables dependent on location were used to determine the effects of growth rate on the model outputs. No sensitivities were run for *S. verreauxi* for age at maturity or growth due to less documented variation (Montgomery et al. 2009). Two further aspects of the model to be investigated were the effect of increasing and decreasing natural mortality estimates, M, and stock-recruitment steepness values, h. These two parameters are key in determining stock productivity and hence important factors to test the sensitivity of the model to alternative input values (Plagányi et al. 2018).

Table 5.6. Model 1 sensitivity analyses. See Table S5.3 for more details on changes to parameters and model estimates.

Sensitivity parameter	Description
Heatwave strength	Adjusted strength of multiplier
Age at minimum size selectivity	Applied different regional growth data
von Bertalanffy growth parameters	Applied different regional growth data
Natural mortality (*M*)	Increased *M*
Stock-recruitment steepness (*h*)	Increased and decreased *h*

Model 2: Extension of Model 1 with competitive interactions

In addition to considering the environmental-physiological influences as per Model 1, Model 2 is further modified to investigate the potential implications of future competition between the two species (see Tables 5.7 and 5.8). For the *J. edwardsii* species component of extended Model 2, all assumptions and calculations are as for Model 1A, except as described below. For *S. verreauxi*, the recruitment formulations are built in a stepwise manner, adding complexity as the model is developed. As the potential carrying capacity K(ERL) for *S. verreauxi* extending into new areas is unknown, the model is started with a separate carrying capacity to *J. edwardsii*, as well as no competitive interaction yet. As per Model 1A, it is assumed that *S. verreauxi* population growth is facilitated by larval advection and settlement of puerulus into the different spatial zones. However, Model 2A also assumes local self-recruitment occurs, which was previously not included, i.e. the population is assumed to have fully settled and able to complete the full life cycle rather than relying solely on external recruitment via larval advection. Model 2A uses fixed carrying capacity K(ERL) for *S. verreauxi* and assumes local self-recruitment and external recruitment with a fixed number of puerulus recruiting into the four spatial zones. As there are no data to estimate K(ERL) in this model version, the *S. verreauxi* model trajectories reflect relative population trajectories rather than absolute projected biomass.

Table 5.7. Model 2 equations. Parameters in equations are further defined in Table 5.8. Here, *s* denotes the species identifier where *s* = 1 are *Jasus edwardsii* females, *s* = 2 are *J. edwardsii* males and *s* = 3 are combined female and male *Sagmariasus verreauxi*.

Model	Equation	No.
Beverton-Holt stock-recruitment	$R^s_{z,y} = \frac{\alpha^s_{z,y} B^{sp,s}_{z,y-1}}{\beta^s_{z,y} + B^{sp,s}_{z,y-1}}$	33
	$\beta^s_{z,y} = \frac{\left(\eta^s_y \cdot \left(K^{sp,1}_z + K^{sp,3}_z\right)\right)\left(1-5h^s 0.2\right)}{5h^s - 1}$	34
	$\alpha^s_{z,y} = \frac{\beta^s_z + \left(\eta^s_y \cdot \left(K^{sp,1}_z + K^{sp,3}_z\right)\right)}{SPR^1_{virg} + SPR^3_{virg}}$	35
Competitive strength equation	$\eta^1_y = 0.159 \times T_{z,y,t} + 0.504$ $\eta^3_y = 1 - \eta^1_y$	36

Table 5.8. Model 2 variable and parameter definitions, where 'SRL' indicates *Jasus edwardsii* and 'ERL' indicates *Sagmariasus verreauxi*.

Variable/ Parameter	Description	Input/ Computed/ Estimated
$\alpha^s_{z,y}, \beta^s_{z,y}$	Spawning biomass-recruitment relationship parameters for species *s* in zone *z* and year *y* (where *y* includes all years for SRL but only years post-2006 for ERL)	Calculated from equation 34 & 35
$B^{sp,s}_{z,y}$	Spawning biomass of species *s* in zone *z* at the start of year *y*	Calculated from equation 7
η^s_y	Relative competitive ability of species *s* in year *y*	Calculated from equation 36
$T_{z,y,t}$	Projected sea surface temperature	Input

Model 2 scenarios

The alternative model versions are developed as follows (and summarised in Table 5.9):

Model 2A *S. verreauxi* is based on Model 1A but now assumes both self-recruitment from the adults now assumed to be settled in each zone, forming a breeding population, as well as recruitment of puerulus from an external population. Model 2A sets K(ERL) at half of the

carrying capacity for *J. edwardsii* motivated by considering this is the most likely scenario if assuming equal competition between the two species. If equal competition is assumed, the total resource carrying capacity for *J. edwardsii* would be half of what it is currently, with *S. verreauxi* occupying the other half. Carrying capacity is a proxy for more complex ecological processes such as resource availability and use and it is not known to what extent these overlap for the two species. While it is known or strongly suspected that both species prey on sea urchins, the feeding ecology of *S. verreauxi* has been poorly studied (Redd et al. 2008, Byrne & Andrew 2013). Due to a recent divergence between *Jasus* and *Sagmariasus* lineages (Jeffs et al. 2013), as well as similarities in the feeding ecology among spiny lobster species (Booth 2006), it would be appropriate to assume that *J. edwardsii* and *S. verreauxi* have similar resource requirements. Therefore, it is assumed that there is substantial overlap in resource requirements of *S. verreauxi* and *J. edwardsii* in Tasmania.

Model 2B assumes a joint carrying capacity for both species and includes competitive interactions between the species. Here, their relative share of the joint carrying capacity is influenced by their competitive ability. Competitive ability is assumed to influence access to resources and the outcome of competitive interactions is therefore represented in the model through changes to the share of the total carrying capacity for each species in each zone. This adjustment of carrying capacity affects the level of self-recruitment and hence population growth. In this scenario, competitive ability is assumed constant from a base year of 2006 and is independent of SST changes in the future projections.

Model 2C is based on 2B but now assumes temperature dependence in the competitive interaction, where competitive ability and hence carrying capacity is a function of changes in projected SST in each of the zones.

Model 2D is based on 2C and incorporates effects of simulated marine heatwaves, applied as a temperature multiplier.

In theory, with increases in warming, *J. edwardsii* will be more competitive that *S. verreauxi* and this effect should increase and temperature increase.

Table 5.9. Model 2 scenarios, where 'SRL' indicates *Jasus edwardsii* and 'ERL' indicates *Sagmariasus verreauxi*. See Table S5.2 for more details on changes to parameters and model estimates.

Model 2	**Description**
Model 2A	Model 1A for SRL, ERL assume self plus external recruitment
Model 2B	Model 2A with joint K and competition included, where SST does not affect competition
Model 2C	Model 2B with SST effect on competition
Model 2D	Model 2C with heatwave simulations

Model 2 sensitivity tests

Model 2 sensitivity tests are summarised in Table 5.10. For Models 2A and 2B, the effect of increasing and decreasing the stock-recruitment steepness parameter, *h*, on biomass estimates of *J. edwardsii* and *S. verreauxi* was investigated. The effect of the strength of simulated heatwaves on both species projected biomass estimates in Model 2D was also investigated.

Table 5.10. Model 2 sensitivity analyses. See Table S5.4 for more details on changes to parameters and model estimates.

Model 2	**Description**
Stock-recruitment steepness *(h)*	Increased and decreased *h*, applied to Models 2A and 2B
Heatwave strength	Adjusted strength of multiplier, applied to Model 2D

Results

Model 1: Incorporating physiological parameters

Incorporating physiological parameters greatly influenced the outcome of the model projections, with results indicating that future projections are dependent on species, sex and spatial zone (Figure 5.2).

Model 1A included physiological parameters in the model and did not show considerable change in estimated *J. edwardsii* biomass over the projected period (2017-2050) compared to the historical biomass (1970-2017) where temperature was not included in the model dynamics (Figure 5.2, Model 1A). Removing the physiological effect from the model entirely (Model 1B) resulted in slight increases in *J. edwardsii* projected biomass over the projection period (Figure 5.2, Model 1B). Removing the physiological effect from the recruits only resulted in a slightly larger increase in projected biomass of *J. edwardsii*. The effect of simulated plausible heatwave scenarios increased projected biomass substantially for *J.* edwardsii (Figure 5.2, Model 1C).

While these trends were observed for both female and male *J. edwardsii*, there were variations in the magnitude of changes dependent on sex and spatial zone. For example, *J. edwardsii* female model simulations had similar magnitudes of projections over the four spatial zones (Figure 5.2, SRL Females). However, for *J. edwardsii* males, there was a large difference in the effects of different model scenarios on biomass projections between zones 1 and 4, where zones 4 showed large changes in the biomass projections while there was little difference between the scenarios in zone 1 (Figure 5.2, SRL Males).

Slightly different outcomes are projected for *S. verreauxi*. Including the physiological data in Model 1A significantly increases the projected biomass of *S. verreauxi* in all spatial zones, though this varied slightly in magnitude between the zones (Figure 5.2, Model 1A). Removing the physiological parameters from the population (Model 1B) or just the recruitment (Model

1C) equations shows little increase in projected biomass (Figure 5.2). Simulations that include future heatwave scenarios (Model 1D) indicated a similar increase the projected biomass of *S. verreauxi* compared to Model 1A (Figure 5.2).

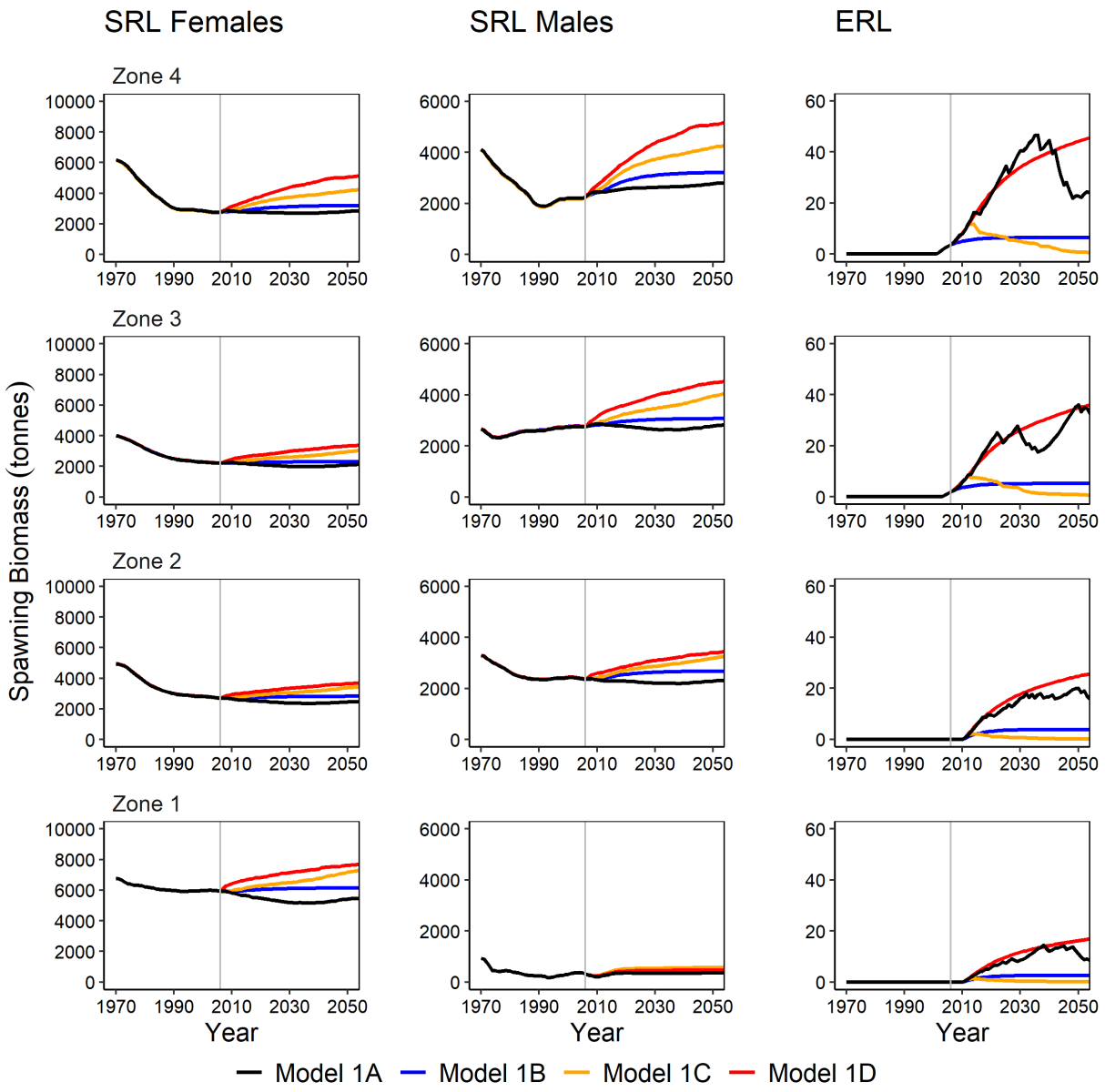

Figure 5.2. Model 1 simulations of the effects of including physiological parameters for lobsters where 'SRL F' are *Jasus edwardsii* females, 'SRL M' are *J. edwardsii* males and 'ERL' are *Sagmariasus verreauxi*. Model simulations include the base physiological Model 1A, a scenario where no physiological parameters are applied (Model 1B), a scenario where the physiological parameter is applied to the adult population only and not to the newly recruiting individuals (Model 1C) and a scenario that includes simulated heatwave effects (Model 1D). The grey dashed line indicates when temperature effects are introduced to the model (2006).

Adjusting the fishing mortality of *J. edwardsii* in the model affected projected biomass of both species (Figure 5.3). Decreasing fishing mortality to zero (Model 1E) results in a small increase in projected biomass of *J. edwardsii* males and females, with no effect on *S. verreauxi* projected biomass. However, increasing the fishing mortality to five times the average fishing mortality in Model 1A, shows simulated declines in *J. edwardsii* projected biomass, but an indirect increase in *S. verreauxi* biomass estimates (Figure 5.3, Model 1F).

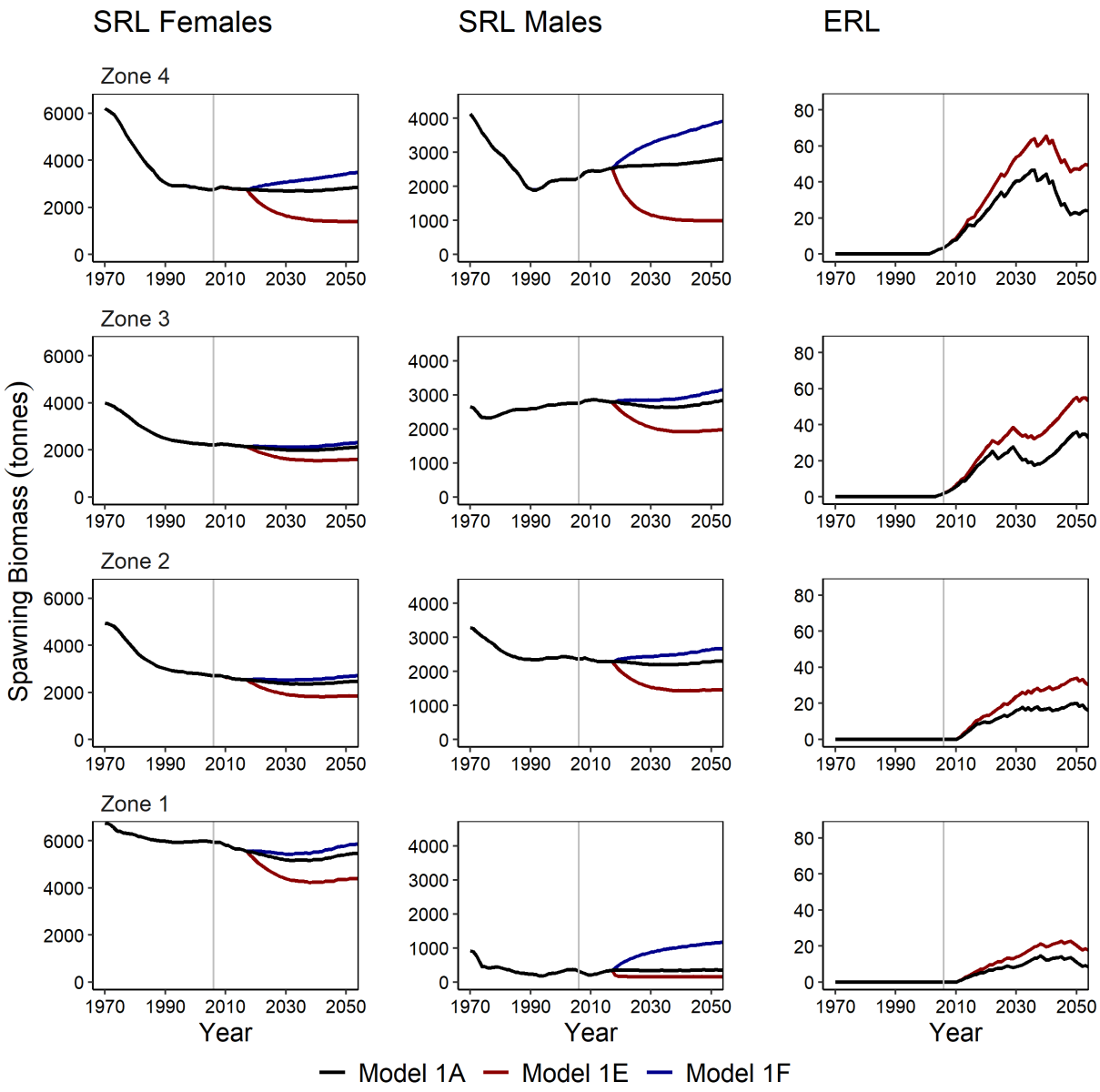

Figure 5.3. Model 1 simulations of the effects of adjusting fishing effort parameters for lobsters where 'SRL F' are *Jasus edwardsii* females, 'SRL M' are *J. edwardsii* males and 'ERL' are *Sagmariasus verreauxi*. Model simulations of the effects of the 'base' scenario (Model 1A), a scenario where no fishing pressure is applied (Model 1E), and a third scenario that includes a high fishing pressure of five times the current average fishing rate (Model 1F). The grey dashed line indicates when temperature effects are introduced to the model (2006). Catch per unit effort data is available up to 2016 and projections of change to fishing mortality begin in 2017.

Adjusting sensitivity parameters had different magnitudes of effect depending on species, sex and spatial zone (Figure 5.4). Changing growth parameters (via changes to von Bertalanffy parameters, adjusting values to Inshore South West (ISW) and Taroona growth parameters from Gardner and Van Putten (2008), see Table S5.3 for adjusted values) for *J. edwardsii* females and males changed the projected biomass differently depending on the spatial zone they occupy. There were opposite effects for changing growth parameters between *J. edwardsii* males and females in terms of spatial zones. For *J. edwardsii* females, adjusting the growth parameters did not change the projections in zone 4 (northern zone) but did substantially affected the projected biomass in zone 1 (southern zone). In contrast, for *J. edwardsii* males, projected biomass changed more in zone 4 than it did in zone 1 as a result of changing growth parameters. Increasing the natural mortality estimate, *M*, by 50% increased, or did not notably affect, projected biomass for all species, sexes and spatial zones (Figure 5.4). Similarly, decreasing the stock recruitment steepness parameter *h* from 0.7 to 0.6, did not greatly affect projected biomass for all species, sexes and spatial zones (Figure 5.4). Note that in Figure 5.4, the Taroona growth adjustment (yellow line) for *J. edwardsii* females in Zone 2 lies below the Model 1A line (black).

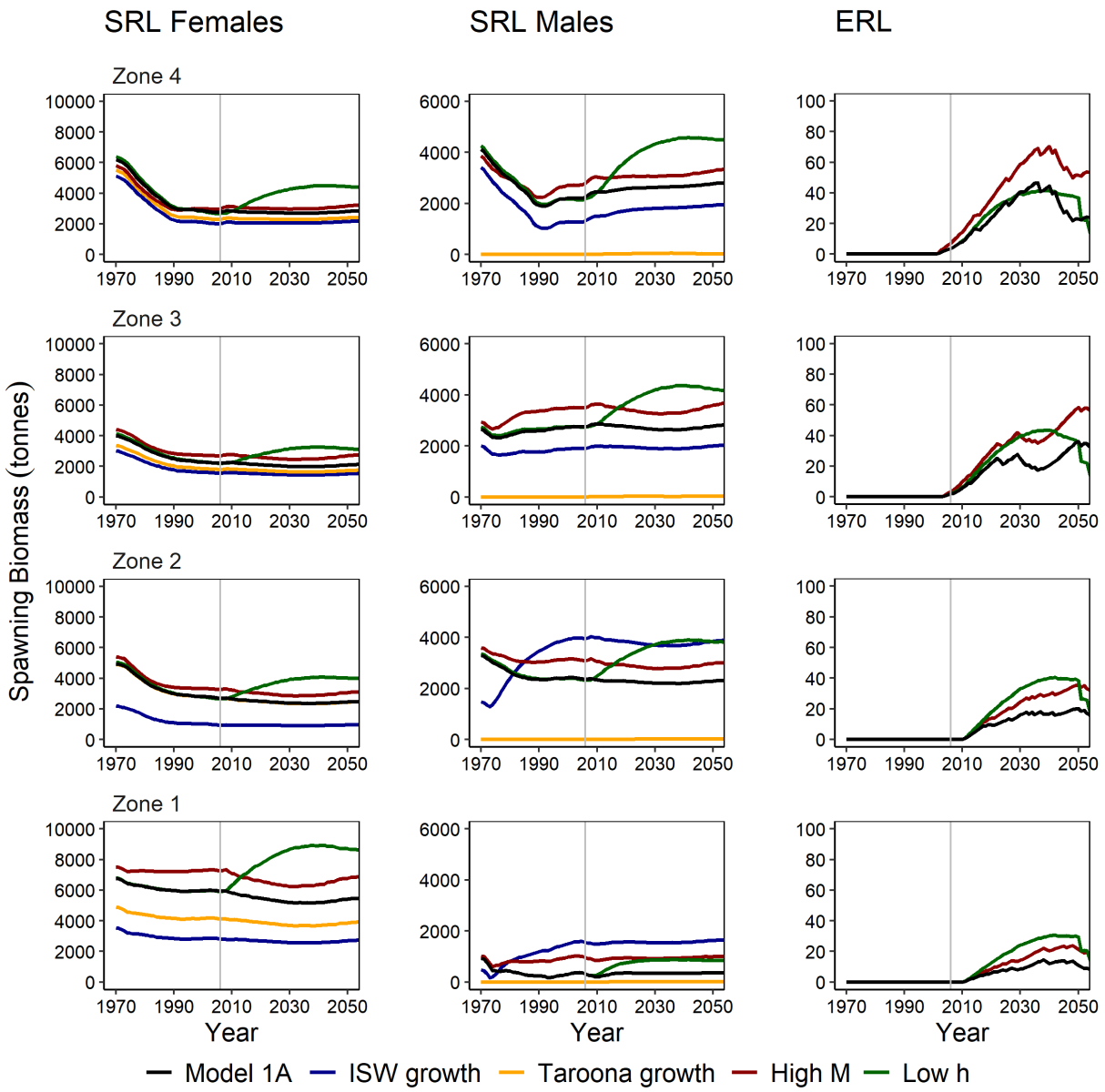

Figure 5.4. Model sensitivity simulations of the effects of different model parameters for lobsters where 'SRL F' are *Jasus edwardsii* females, 'SRL M' are *J. edwardsii* males and 'ERL' are *Sagmariasus verreauxi*. Model sensitivity simulations are all relative to the 'base' scenario (Model 1A), where changes to the growth parameters is applied (Inshore South West (ISW) growth and Taroona growth), as well as altering the natural mortality, *M*, value to 50% higher than the base scenario (High M) and the stock recruitment steepness, *h*, to a decreased value (Low h). The grey dashed line indicates when temperature effects are introduced to the model (2006).

Adjusting the strength of the heatwave simulation parameter changed the projected biomass of both species (Figure 5.5). For *J. edwardsii*, a moderate heatwave value resulted in the highest projected biomass, with high (Model 1D strong) and low (Model 1D weak) heatwave values having lower projected biomass, though these values were still higher than the base model with no heatwave simulation. For *S. verreauxi*, the strong heatwave simulation showed a slightly higher projected biomass over the moderate simulation, while the low heatwave strength multiplier results in projected biomass that was lower than the base model (Model 1A) with no heatwave effect in the short term, though this appears to reverse closer to 2050 (Figure 5.5).

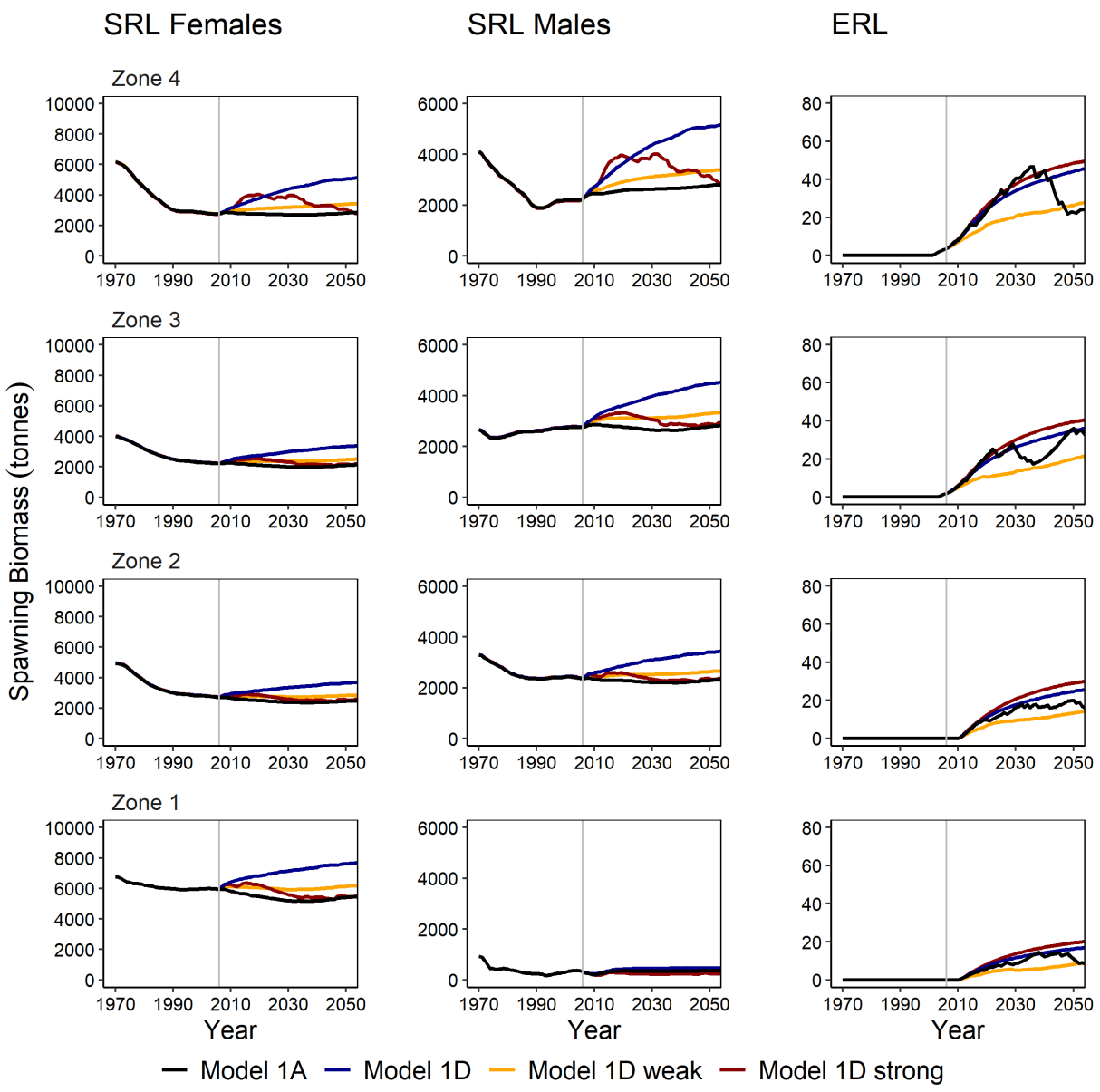

Figure 5.5. Model sensitivity simulations of the effects of heatwave multiplier strength for lobsters where 'SRL F' are *Jasus edwardsii* females, 'SRL M' are *J. edwardsii* males and 'ERL' are *Sagmariasus verreauxi*. Model sensitivity simulations are based on the base model (Model 1A) and the heatwave simulation model (Model 1D) and include sensitivities of weakening the heatwave simulation strength (Model 1D weak) or strengthening the heatwave simulation strength (Model 1D strong). The grey dashed line indicates when temperature effects are introduced to the model (2006).

Model 2: Incorporating competitive interactions

To be able to compare Model 1 and Model 2, both Model 1A and Model 2 scenarios are plotted in Figure 5.6. For *J. edwardsii* (both males and females), Model 1A and 2A show the same results as altering the self-recruitment of *S. verreauxi* only influenced their species simulation (Figure 5.6). Incorporating a joint carrying capacity and competition between the species (Model 2B) resulted in a simulated reduction in *J. edwardsii* projected biomass for both males and females. The results are very similar for Model 2C, which also incorporated competitive ability into the model, though this scenario is temperature dependent. Heatwave simulations (Model 2D) for *J. edwardsii* show varied results from little effects in zone 4, to more substantial effects in zones 1-3. Interestingly, the heatwave effects appeared to modify and, in the case of zone 4, completely moderate the effect of a combined carrying capacity and competition on the projected biomass of *J. edwardsii*. Again, *S. verreauxi* showed different patterns of response to changing model scenarios (Figure 5.6, 'ERL'). In Model 2A, changing *S. verreauxi* recruitment from external only to external and self-recruitment slightly increased the projected biomass from Model 1A. Further, incorporating a joint carrying capacity and competitive interaction (Model 2B) between the species greatly increased the projected biomass of *S. verreauxi*. Again, as observed for *J. edwardsii*, the temperature dependence of the competitive interaction did not really affect projected biomass between Model 2B and 2C. In the case of simulated changes via introducing heatwave scenarios (Model 2D), projected biomass of *S. verreauxi* greatly increased over all spatial zones (Figure 5.6).

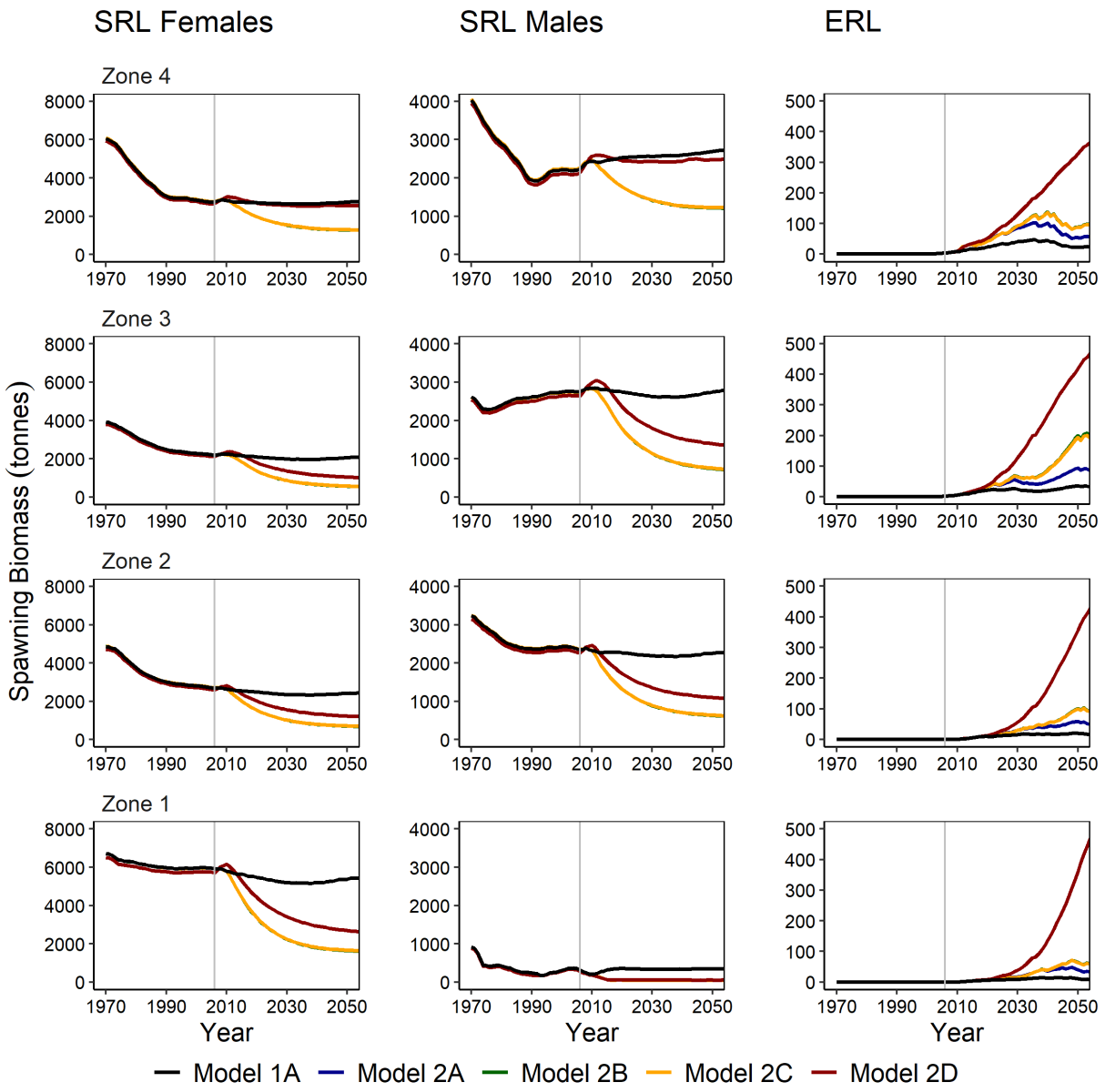

Figure 5.6. Model 2 simulations of the effects of including a joint carrying capacity *K* and competitive interactions for lobsters where 'SRL F' are *Jasus edwardsii* females, 'SRL M' are *J. edwardsii* males and 'ERL' are *Sagmariasus verreauxi*. Model 2 scenarios are compared to Model 1A, where the model is then modified to include self-recruitment for *S. verreauxi* (Model 2A), a joint carrying capacity with a non-temperature dependent competitive interaction (Model 2B), a temperature-dependent competitive interaction (Model 2C) and simulated heatwave effects (Model 2D). The grey dashed line indicates when temperature effects are introduced to the model (2006)

Model 2A adopts a medium estimated ERL(K) as explained above. By decreasing this value (Figure 5.7, ‘Low’ scenario), projected *S. verreauxi* biomass decreased very slightly compared to the medium estimated value. However, by increasing ERL(K) (Figure 5.7, ‘High’ scenario), biomass of *S. verreauxi* is projected to greatly increase above the medium estimated ERL(K). Again, the magnitude of the simulated outcome is dependent on the spatial zone, with higher biomass projected in the northern areas (zones 3-4) and lower projected biomass in the south of the region (zones 1-2).

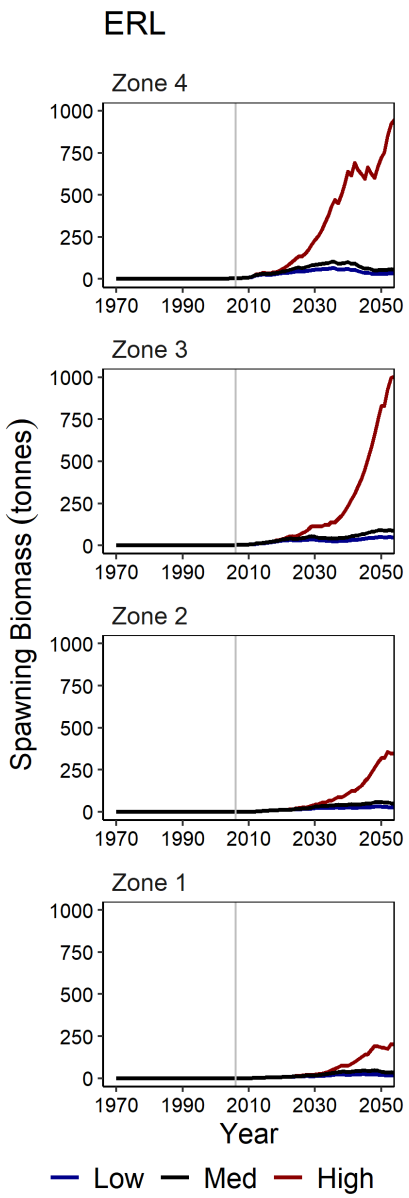

Figure 5.7. Use of different carrying capacity for *Sagmariasus verreauxi* (ERL). Model 2A is considered the medium *S. verreauxi* carrying capacity, ERL(K), 'Low' indicates lower values for ERL(K) and 'High' indicates a higher ERL(K). The grey dashed line indicates when temperature effects are introduced to the model (2006).

Adjusting the stock-recruitment steepness, *h*, parameter values affected *J. edwardsii* and *S. verreauxi* differently (Figure 5.8). Increasing (h 0.8) or decreasing (h 0.6) the stock-recruitment steepness (from the base value of 0.7) for *J. edwardsii* does not significantly change projected biomass. However, for *S. verreauxi*, while decreasing *h* does not change the projected biomass, increasing *h* results in projected declines in biomass estimates in all spatial zones (Figure 5.8).

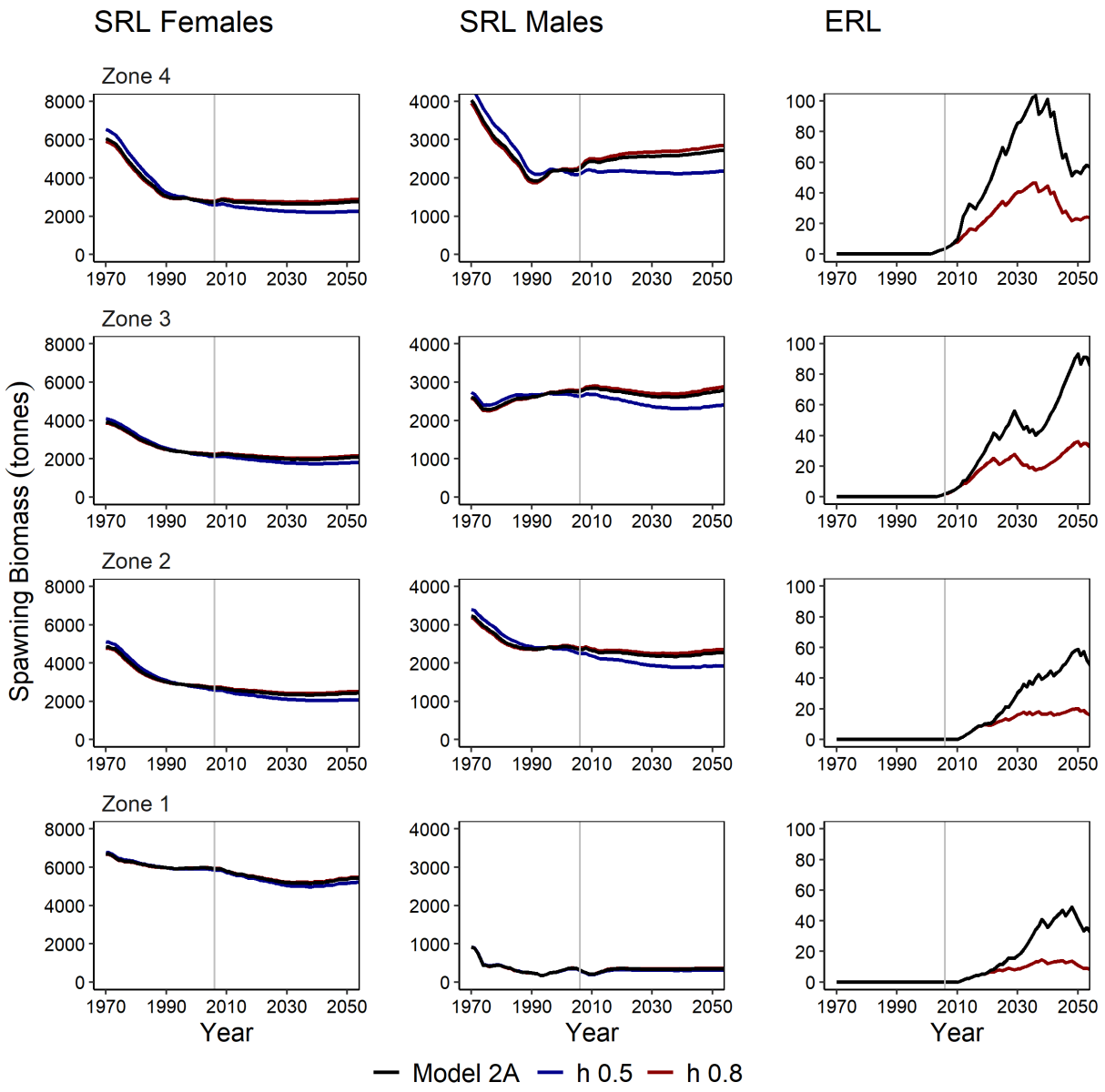

Figure 5.8. Model 2A sensitivity simulations of the effects of adjusting stock-recruitment parameters for lobsters where 'SRL F' are *Jasus edwardsii* females, 'SRL M' are *J. edwardsii* males and 'ERL' are *Sagmariasus verreauxi*. Adjustment of stock recruitment steepness *h* values in Model 2A where 'h 0.5' indicates a decreased value and 'h 0.8' indicates an increased value. The grey dashed line indicates when temperature effects are introduced to the model (2006).

Similar to the above sensitivities for Model 2A, adjusting the stock-recruitment steepness, *h*, parameter values affected *J. edwardsii* and *S. verreauxi* differently for Model 2B (Figure 5.9). Again, increasing (h 0.8) or decreasing (h 0.5) the stock-recruitment steepness for *J. edwardsii* did not significantly change projected biomass. However, for *S. verreauxi*, while decreasing *h* did not change the projected biomass, increasing *h* resulted in projected declines in biomass estimates in all spatial zones (Figure 5.9).

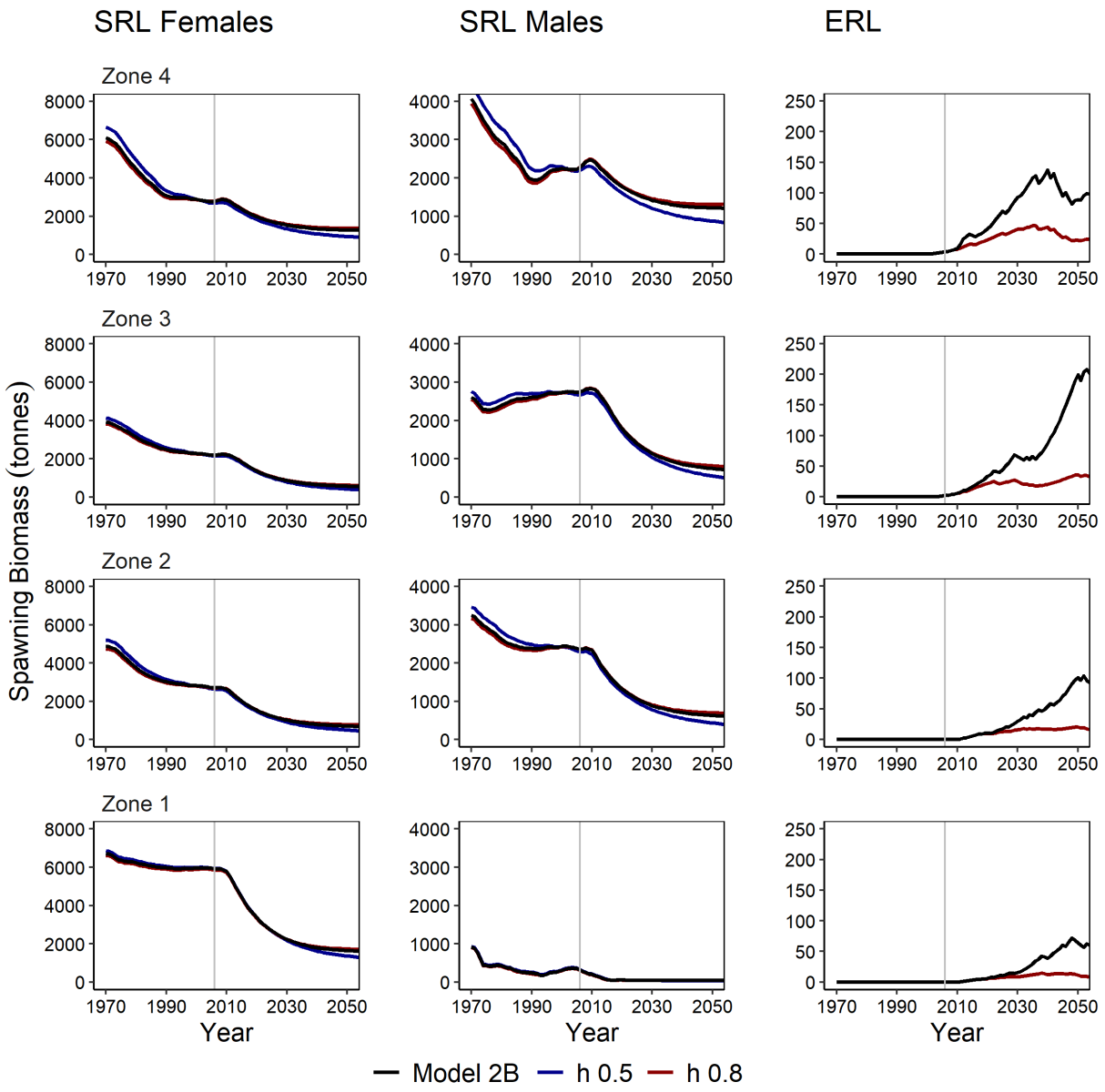

Figure 5.9. Model 2B sensitivity simulations of the effects of adjusting stock-recruitment parameters for lobsters where 'SRL F' are *Jasus edwardsii* females, 'SRL M' are *J. edwardsii* males and 'ERL' are *Sagmariasus verreauxi*. Adjustment of stock recruitment steepness *h* values in Model 2B where 'h 0.5' indicates a decreased value and 'h 0.8' indicates an increased value relative to the base case (Model 2B). The grey dashed line indicates when temperature effects are introduced to the model (2006).

Discussion

Here, it was found that including temperature-dependent physiological tolerance and competitive interaction data in MICE greatly affects the model biomass estimates for both species. While physiological data directly affected the species, the inclusion of competitive interactions changes the magnitude or reverses the potential direction of biomass change. These results indicate that including physiological data into models is important to be able to accurately address changes due to a changing climate, especially those due to indirect effects of species interactions that can result in complicated and unpredictable changes.

Incorporating physiological parameters (Model 1)

Including physiological parameters greatly changed biomass projections for both species, compared to when it was excluded. For *J. edwardsii*, including physiological parameters resulted in little change in projected biomass from historical trajectories as future SST projections were still below thermal optima for *J. edwardsii* (Twiname et al. in prep-b), resulting in a negative effect on projected biomass (Figure 5.2). However, when the physiological data was removed from the model, there was a small increase in projected biomass. When heatwave simulations are included, projected biomass increased significantly (Figure 5.2). This is due to the effect of temperature in the model, where heatwave simulations raised SST projections closer to optimal for the species (Twiname et al. in prep-b), thereby positively influencing individual and population growth. A particularly noteworthy result in Model 1 is the difference between full, partial and no physiological data incorporation in the model. With physiological data included, projected biomass of *J. edwardsii* (males and females) is predicted remain at levels similar to recent historical biomass hind-casts (Figure 5.2). Without physiological parameters included in the model, projected biomass increased slightly in future. But when physiological parameters are included in the population equations, but not the recruitment equations, there was a larger increase in projected biomass (Figure 5.2). This

is because, based on available information, the model assumes a relatively strong effect of temperature on the new recruits that negatively affects projected biomass, while there is an opposite effect on the population, i.e. the temperatures are still too cool for the puerulus stage to do well, while this does not affect the older life stages as strongly.

In contrast to *J. edwardsii*, *S. verreauxi* exhibited increases in projected biomass when physiological data were included compared to when it was not (Figure 5.2). When no physiological data are included, there was a very small increase in projected biomass of *S. verreauxi* across all zones. However, when including physiological effects, projected biomass increased 2-4 fold depending on the spatial zone (Figure 5.2). This large increase in projected biomass indicates that even relatively small increases in temperature may have a disproportionately positive influence on projected biomass. Including heatwave scenarios had a different result for *S. verreauxi* than *J. edwardsii*, where heatwave simulations did not significantly increase *S. verreauxi* projected biomass levels above those where physiological data is included (Figure 5.2). This is interesting as a larger increase in projected biomass with heatwave simulations would be expected, as observed for *J. edwardsii*. This might again be attributed to the level of warming and the thermal tolerance of the species, whereby *S. verreauxi* have higher thermal tolerances than *J. edwardsii* and therefore the projected SST is even further from their performance optima, with room to further increase performance and projected biomass at higher temperatures. As for *J. edwardsii*, there was an interesting effect of partial application of the physiological data, however it was an opposite effect for *S. verreauxi*. Here, when physiology was included, there was a relatively higher projected biomass, with no physiology, it was lower and with physiology applied to just the population and not the recruits there was an even lower projected biomass (Figure 5.2). This result indicates that there was a large positive influence of temperature on *S. verreauxi* recruits, and that this had a positive effect on recruitment and hence the population. Species that are extending their ranges into

cooler water areas have to overcome the barrier of larval and early juvenile over-wintering (Figueira et al. 2009). However, the model results indicate that temperatures are sufficient to allow overwintering survival of *S. verreauxi* recruits and that they could potentially contribute significantly to population growth of *S. verreauxi* in Tasmania,

Incorporating competitive interactions (Model 2)

Including competition for resources altered the population dynamics of the two lobster species observed in Model 1. For *J. edwardsii*, including a joint carrying capacity and competitive interaction resulted in decreased projected biomass (Figure 5.6). This is interesting as while their thermal tolerances are lower than that of *S. verreauxi* (Twiname et al. in prep-b), their competitive ability increases with temperature above those of their thermal optima (Twiname et al. in prep-a) and therefore it would have been expected to see increases in projected biomass as they outcompete *S. verreauxi*. However, it appears that the higher magnitude of the thermal tolerances of *S. verreauxi* may outweigh the competitive advantage that *J. edwardsii* have in the model. In addition, this negative affect of competition on *J. edwardsii* is somewhat mitigated when heatwave simulations are included, with implications for both species. Once winter temperatures reach above those critical for puerulus survival, there could potentially be a rapid change in species composition in Tasmania. While it was assumed that there is substantial overlap in resource use by the two species, the feeding ecology of *S. verreauxi* is poorly understood (Byrne & Andrew 2013). Therefore, we do not know if or to what extent the species will fill the same ecological niche that *J. edwardsii* currently occupy.

Results for *S. verreauxi* projected biomass in Model 2 scenarios showed generally opposite effects to those observed for *J. edwardsii*. Introducing self-recruitment of *S. verreauxi* increased projected biomass as a result of increased recruitment potential (Figure 5.6, Model 2A). By introducing a joint carrying capacity for the two species, *S. verreauxi* projected biomass increased as a result. Interestingly, the difference between Models 2B (joint K and

temperature independent competition) and 2C (joint K and temperature-dependent competition) was marginal. This indicates that the model did not predict substantially different future biomass between the two scenarios, presumably because the temperature ranges tested, based on available SST projections, were not sufficiently high enough to result in a larger change. The effect of heatwave simulations is striking on the change in projected biomass, with a more than four-fold increase in projected biomass across all spatial zones. This suggests that with more warming and moderate heatwave effects, *S. verreauxi* biomass has the potential to increase considerably across all spatial zones in Tasmania.

Model scenarios

Adjusting fishing effects in Model 1 results in expected projected biomass changes; increasing fishing mortality and hence catch decreases *J. edwardsii* projected biomass, while decreasing fishing mortality results in increased projected biomass of *J. edwardsii* (Figure 5.3). Increased fishing mortality was set at a level of five times the average fishing used in Model 1A. This did not translate to a fivefold decrease in projected biomass. Similarly, decreasing fishing mortality to zero only increased projected biomass a small amount. This result suggests that changes in fishing mortality and catch do not necessarily translate to equivalent changes in lobster biomass. For *S. verreauxi*, while no fishing mortality is applied to this species, there is a modest increase in projected biomass when a high fishing scenario is applied to *J. edwardsii*. This increase in *S. verreauxi* projected biomass is an indirect effect of increased pressure on *J. edwardsii*, decreasing their projected biomass allowing an increase in *S. verreauxi* biomass estimates. These results indicate that the model would be useful in quantifying the impact of different fishing levels on projected populations due to changes in fishing mortality.

Another interesting outcome of this modelling study and the use of different spatial zones is the magnitude of some model responses in these different areas. This is in part due to different *J. edwardsii* growth equations used in the different spatial zones. The models show higher

projected biomass in the northern zones compared to the southern. This is due to lobsters having high growth rates in the warmer waters of northern Tasmania (Gardner & Van Putten 2008). Additionally, in the southern spatial zones there is a high ratio of female to male *J. edwardsii*. This is due to many female lobsters not reaching legal size and remaining in the spawning stock biomass. Changes to projected biomass under different scenarios also changes disproportionately. Larger changes were observed in the northern zones, likely as a result of higher ambient temperatures and hence a small amount of warming pushes temperatures closer to those that are optimal for *J. edwardsii*. In the southern zones, there is relatively little change in projected biomass when including physiological measures compared to scenarios where they are not. This is likely due to temperatures being far below those that are optimal and so small amounts of warming are not resulting in as significant changes as in the warmer northern zones. In *S. verreauxi*, the differences between zones are due to different temperatures based on the effect of temperature on survival. As no area-dependent alternative growth parameters were available for *J. edwardsii*, the difference between the zones is an outcome of the thermal tolerance data included in the mortality term.

Sensitivity analyses

Sensitivity parameters investigated using Model 1 showed different magnitudes of response dependent on species, sex and spatial zone (Figure 5.4). Changing the growth model parameters for *J. edwardsii* offset biomass projections from Model 1A, with the largest effect being difference in the magnitude of change between zones and sexes (Figure 5.4, Inshore South Eest (ISW) and Taroona growth). For *J. edwardsii* females, little change was observed between projections in Zone 4 (north) but there was large variation between model estimates in Zone 1 (south). The opposite was seen in *J. edwardsii* males where larger variation was exhibited in Zone 4 (north) than Zone 1 (south). Altering the natural mortality value had similar effects, where larger differences were observed between male and female *J. edwardsii*. Changing the

stock recruitment steepness parameter altered biomass projections slightly. For *S. verreauxi* sensitivities, only changes in natural mortality and stock-recruitment steepness adjusted biomass projections. Increasing *M* and decreasing *h* both resulted in increases in *S. verreauxi* biomass.

Adjusting the strength of the heatwave parameter had different effects on the magnitude of projected biomass changes. By weakening the heatwave simulation, there was a smaller increase in biomass estimates compared to the model heatwave simulation in Model 1D. When a strong heatwave simulation was applied, there was a steeper initial increase in projected biomass before it peaked and declined to projected biomass estimates similar to those with no heatwave effects. This suggests that small to moderate heatwave effects may be beneficial for *J. edwardsii* population growth, but stronger heatwave effects may negatively affect projected biomass by increasing temperatures above those that are optimal for the species (Twiname et al. in prep-b). Alternatively, for *S. verreauxi*, increasing heatwave strength from low to high showed continual increases in projected biomass. This is likely due to *S. verreauxi* having higher thermal tolerances than *J. edwardsii* and hence stronger heatwave effects positively influence their population growth.

In Model 2A, the magnitude of future projected biomass is determined by the magnitude of the carrying capacity that is used (Figure 5.7). Investigating the effects of adjusting the stock-recruitment steepness parameters *h* has a different effect on each of the two species. In *J. edwardsii*, increasing and decreasing *h* has little effect on model biomass outputs. However, in *S. verreauxi*, decreasing *h* has little effect while increasing *h* increases biomass estimates considerably because this scenario represents one in which relatively high recruitment levels can be achieved even at relatively low spawning biomass levels. In Model 2B sensitivities, similar results are observed when adjusting *h*, where there is little effect on model outputs for

J. edwardsii but increasing *h* has a significant effect on *S. verreauxi* estimates with effect size affected by spatial zone.

Future model directions

This model includes a mechanistic approach by including temperature dependent physiological and competition measures. Future models could expand on this framework by including predator-prey interactions which would assist in exploring hypotheses as to how the two spiny lobsters would fit into their wider community. Refining and expanding the coding of the MICE with more detailed climate and oceanographic model outputs could provide a more accurate biomass estimate for both lobster species. For example, by including the outputs from an oceanographic model that predicts changes in spiny lobster settlement in a changing climate, the biomass estimates of *S. verreauxi* would be more accurate as it is likely that population growth of this species is currently dependent on puerulus recruitment into Tasmania.

Conclusions

This study advances understanding of the direct and indirect effects of a range-shifting species in a new environment. Here it is shown that including a mechanistic aspect into models can greatly influence the projected outcomes, and that accounting explicitly for physiological influences on population dynamics in models may improve the accuracy of predicted future changes as a result of species range shifts. Heatwave scenarios increased projected biomass for both species, and in some cases appeared to mediate the negative effects of competition on *J. edwardsii*. Overall, model projections predict increases in biomass of *S. verreauxi* across all spatial zones along the east coast of Tasmania, despite thermal tolerances of physiological performance measures and competitive interactions that would suggest that *J. edwardsii* should be competitively superior in the near future under ocean warming conditions.

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Supplementary materials

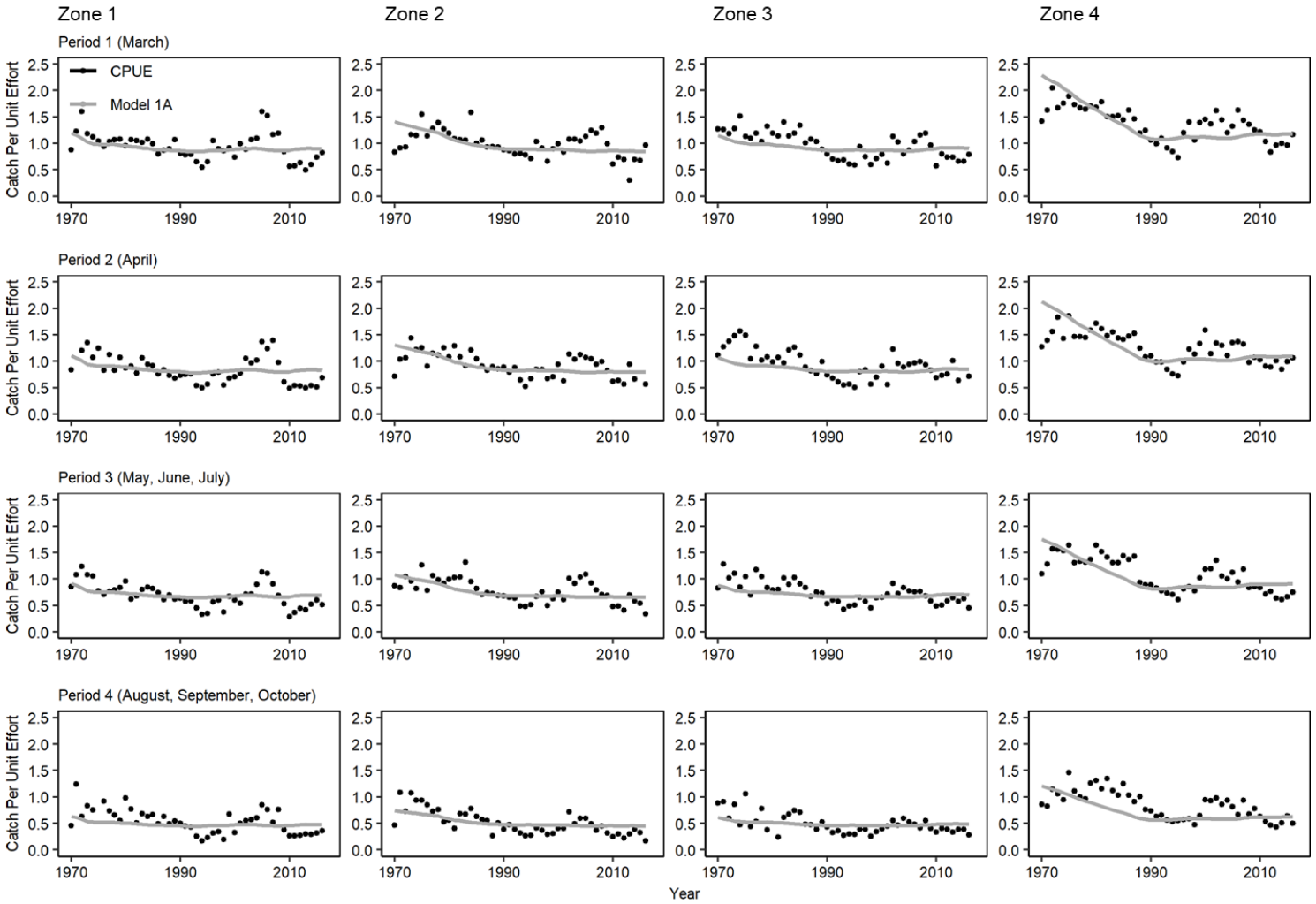

Figure 5.1. Model fit for periods 1-4, where the black dots indicate historical catch per unit effort (CPUE) from the commercial Southern Rock Lobster Fishery, and the grey line indicates the model hind cast projection.

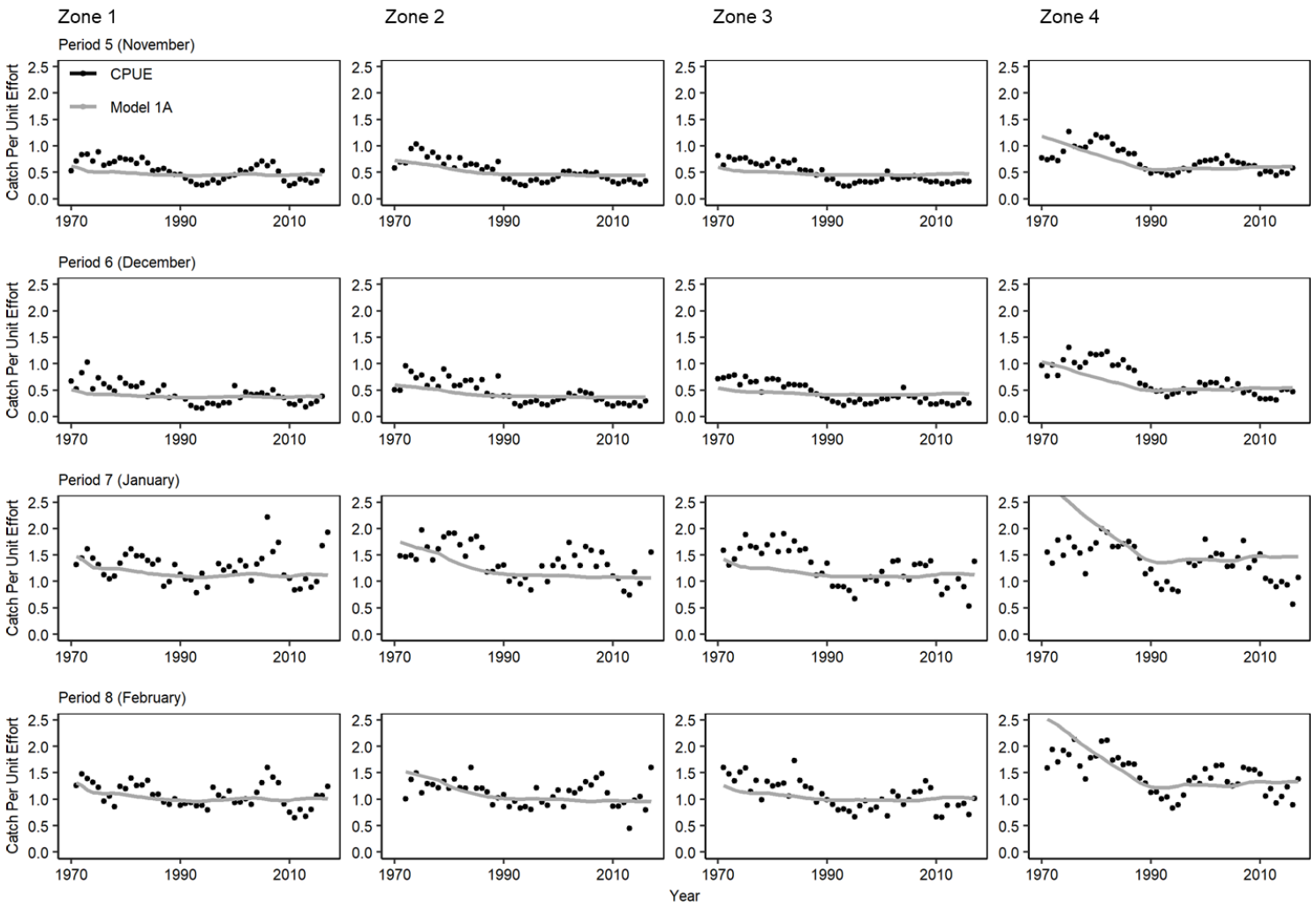

Figure 5.2. Model fits for periods 5-8, where the black dots indicate historical catch per unit effort (CPUE) from the commercial Southern Rock Lobster Fishery, and the grey line indicates the model hind cast projection.

Table 5.1. Summary of Model 1 parameter estimates and fixed inputs, where 'SRL F' indicates *Jasus edwardsii* females, 'SRL M' indicated *J. edwardsii* males and 'ERL' indicates *Sagmariasus verreauxi* (combined sexes). Changes to parameters are highlighted in bold.

	Model 1A – Includes physiology			Model 1B – No physiology			Model 1C – No physiology on recruits		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter									
K(SRL) Zone 1	7678.657	7677.012	7680.303	7678.657	7677.012	7680.303	7678.657	7677.012	7680.303
K(SRL) Zone 2	8225.546	8223.876	8227.216	8233.776	8232.106	8235.446	8225.546	8223.876	8227.216
K(SRL) Zone 3	6650.185	6648.514	6651.856	6692.883	6691.212	6694.554	6650.185	6648.514	6651.856
K(SRL) Zone 4	10331.988	10330.324	10333.652	10326.823	10325.159	10328.488	10331.988	10330.324	10333.652
K (ERL)/per zone	20. 086			20.086			20.086		
M SRL (fixed)	0.00833			0.00833			0.00833		
M ERL (fixed)	0.0058			0.0058			0.0058		
h SRL (fixed)	0.7			0.7			0.7		
h ERL (fixed)	0.7			0.7			0.7		
Likelihood contributions									
Period	Value	sigma	q	Value	sigma	q	Value	sigma	q
1	-178.274	0.235	2.23E-04	-177.997	0.235	2.23E-04	-171.837	0.243	2.22E-04
2	-172.150	0.240	2.10E-04	-171.960	0.240	2.10E-04	-166.701	0.247	2.09E-04
3	-160.281	0.259	5.90E-05	-160.264	0.259	5.90E-05	-152.799	0.269	5.86E-05
4	-100.190	0.354	4.18E-05	-99.676	0.355	4.17E-05	-95.225	0.364	4.15E-05
5	-135.734	0.295	1.25E-04	-135.720	0.295	1.24E-04	-130.419	0.303	1.24E-04
6	-96.030	0.364	1.01E-04	-95.996	0.364	1.01E-04	-91.212	0.373	1.00E-04
7	-147.191	0.270	2.75E-04	-146.307	0.271	2.74E-04	-141.208	0.279	2.72E-04
8	-198.841	0.208	2.50E-04	-198.750	0.208	2.49E-04	-192.815	0.215	2.47E-04
Total	-1188.690			-1186.670			-1142.220		
Fixed parameters									
Heatwave multiplier	1			1			1		
SRL F									
L_∞ Zone 1	107.4			107.4			107.4		

L_∞ Zone 2	107.4			107.4			107.4		
L_∞ Zone 3	127.39			127.39			127.39		
L_∞ Zone 4	147.79			147.79			147.79		
κ Zone 1	0.407			0.407			0.407		
κ Zone 2	0.407			0.407			0.407		
κ Zone 3	0.1701			0.1701			0.1701		
κ Zone 4	0.3029			0.3029			0.3029		
S Zone 1	9			9			9		
S Zone 2	9			9			9		
S Zone 3	10			10			10		
S Zone 4	4			4			4		
SRL M									
L_∞ Zone 1	122.28			122.28			122.28		
L_∞ Zone 2	122.28			122.28			122.28		
L_∞ Zone 3	178.12			178.12			178.12		
L_∞ Zone 4	184.26			184.26			184.26		
κ Zone 1	0.459			0.459			0.459		
κ Zone 2	0.459			0.459			0.459		
κ Zone 3	0.1390			0.1390			0.1390		
κ Zone 4	0.2601			0.2601			0.2601		
S Zone 1	5			5			5		
S Zone 2	5			5			5		
S Zone 3	7			7			7		
S Zone 4	3			3			3		
ERL									
L_∞	239.77			239.77			239.77		
κ	00.13			00.13			00.13		
S	5			5			5		

	Model 1D – Heatwave			Model 1E – High fishing mortality			Model 1F – Zero fishing mortality		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter									
K(SRL) Zone 1	7678.657	7677.011	7680.303	7678.657	7677.012	7680.303	7678.657	7677.012	7680.303
K(SRL) Zone 2	8252.735	8251.062	8254.409	8224.724	8223.054	8226.394	8225.546	8223.876	8227.216
K(SRL) Zone 3	6684.856	6683.182	6686.531	6649.520	6647.849	6651.191	6650.185	6648.514	6651.856
K(SRL) Zone 4	10330.955	10329.288	10332.622	10330.955	10329.291	10332.619	10331.988	10330.324	10333.652
K (ERL)/per zone	20.086			20.086			20.086		
M SRL (fixed)	0.00833			0.00833			0.00833		
M ERL (fixed)	0.0058			0.0058			0.0058		
h SRL (fixed)	0.7			0.7			0.7		
h ERL (fixed)	0.7			0.7			0.7		
Likelihood contributions									
Period	Value	sigma	q	Value	sigma	q	Value	sigma	q
1	-153.760	0.268	2.16E-04	-178.274	0.235	2.23E-04	-178.272	0.235	2.23E-04
2	-151.169	0.269	2.04E-04	-172.151	0.240	2.10E-04	-172.147	0.240	2.10E-04
3	-135.248	0.295	5.70E-05	-160.283	0.259	5.90E-05	-160.277	0.259	5.90E-05
4	-82.508	0.389	4.03E-05	-100.190	0.354	4.18E-05	-100.187	0.354	4.18E-05
5	-113.232	0.332	1.20E-04	-135.734	0.295	1.25E-04	-135.736	0.295	1.25E-04
6	-76.379	0.404	9.74E-05	-96.030	0.364	1.01E-04	-96.030	0.364	1.01E-04
7	-130.706	0.296	2.65E-04	-147.189	0.270	2.75E-04	-147.199	0.270	2.75E-04
8	-175.891	0.236	2.41E-04	-198.879	0.208	2.50E-04	-198.680	0.208	2.50E-04
Total	-1018.890			-1188.730			-1188.530		
Fixed parameters									
Heatwave multiplier	**1.3**			1			1		
SRL F									
L_∞ Zone 1	107.4			107.4			107.4		
L_∞ Zone 2	107.4			107.4			107.4		
L_∞ Zone 3	127.39			127.39			127.39		

L_∞ Zone 4	147.79			147.79			147.79		
κ Zone 1	0.407			0.407			0.407		
κ Zone 2	0.407			0.407			0.407		
κ Zone 3	0.1701			0.1701			0.1701		
κ Zone 4	0.3029			0.3029			0.3029		
S Zone 1	9			9			9		
S Zone 2	9			9			9		
S Zone 3	10			10			10		
S Zone 4	4			4			4		
SRL M									
L_∞ Zone 1	122.28			122.28			122.28		
L_∞ Zone 2	122.28			122.28			122.28		
L_∞ Zone 3	178.12			178.12			178.12		
L_∞ Zone 4	184.26			184.26			184.26		
κ Zone 1	0.459			0.459			0.459		
κ Zone 2	0.459			0.459			0.459		
κ Zone 3	0.1390			0.1390			0.1390		
κ Zone 4	0.2601			0.2601			0.2601		
S Zone 1	5			5			5		
S Zone 2	5			5			5		
S Zone 3	7			7			7		
S Zone 4	3			3			3		
ERL									
L_∞	239.77			239.77			239.77		
κ	00.13			00.13			00.13		
S	5			5			5		

Table 5.2. Summary of Model 2 parameter estimates and fixed inputs, where 'SRL F' indicates *Jasus edwardsii* females, 'SRL M' indicated *J. edwardsii* males and 'ERL' indicates *Sagmariasus verreauxi* (combined sexes). Changes to parameters are highlighted in bold.

	Model 2A – ERL self-recruitment			Model 2B – Joint K			Model 2C – Temperature-independent competition		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter									
K(SRL) Zone 1	7641.124	7639.478	7642.770	7641.124	7639.478	7642.770	7635.777	7634.112	7637.442
K(SRL) Zone 2	8087.703	8086.033	8089.373	8087.703	8086.033	8089.373	8112.813	8111.136	8114.490
K(SRL) Zone 3	6544.629	6542.958	6546.300	6544.629	6542.958	6546.300	6527.635	6525.957	6529.313
K(SRL) Zone 4	10096.055	10094.390	10097.719	10096.055	10094.390	10097.719	10159.861	10158.191	10161.530
K (ERL)/per zone	90.017			90.017			90.017		
M SRL (fixed)	0.00833			0.00833			0.00833		
M ERL (fixed)	0.0058			0.0058			0.0058		
h SRL (fixed)	0.7			0.7			0.7		
h ERL (fixed)	0.7			0.7			0.7		
Likelihood contributions									
Period	Value	sigma	q	Value	sigma	q	Value	sigma	q
1	-178.111	0.235	2.25E-04	-178.111	0.235	2.25E-04	-181.536	0.231	2.26E-04
2	-171.652	0.240	2.11E-04	-171.652	0.240	2.11E-04	-174.791	0.236	2.12E-04
3	-159.605	0.260	5.93E-05	-159.605	0.260	5.93E-05	-165.692	0.251	5.96E-05
4	-99.450	0.355	4.20E-05	-99.450	0.355	4.20E-05	-103.751	0.347	4.23E-05
5	-134.185	0.297	1.25E-04	-134.185	0.297	1.25E-04	-137.469	0.292	1.26E-04
6	-94.623	0.367	1.02E-04	-94.623	0.367	1.02E-04	-97.785	0.361	1.02E-04
7	-147.801	0.269	2.76E-04	-147.801	0.269	2.76E-04	-148.842	0.268	2.79E-04
8	-198.838	0.208	2.51E-04	-198.838	0.208	2.51E-04	-196.922	0.210	2.54E-04
Total	-1184.260			-1184.260			-1206.690		
Fixed parameters									
Heatwave multiplier	1			1			1		
SRL F									

L_∞ Zone 1	107.4			107.4			107.4		
L_∞ Zone 2	107.4			107.4			107.4		
L_∞ Zone 3	127.39			127.39			127.39		
L_∞ Zone 4	147.79			147.79			147.79		
κ Zone 1	0.407			0.407			0.407		
κ Zone 2	0.407			0.407			0.407		
κ Zone 3	0.1701			0.1701			0.1701		
κ Zone 4	0.3029			0.3029			0.3029		
S Zone 1	9			9			9		
S Zone 2	9			9			9		
S Zone 3	10			10			10		
S Zone 4	4			4			4		
SRL M									
L_∞ Zone 1	122.28			122.28			122.28		
L_∞ Zone 2	122.28			122.28			122.28		
L_∞ Zone 3	178.12			178.12			178.12		
L_∞ Zone 4	184.26			184.26			184.26		
κ Zone 1	0.459			0.459			0.459		
κ Zone 2	0.459			0.459			0.459		
κ Zone 3	0.1390			0.1390			0.1390		
κ Zone 4	0.2601			0.2601			0.2601		
S Zone 1	5			5			5		
S Zone 2	5			5			5		
S Zone 3	7			7			7		
S Zone 4	3			3			3		
ERL									
L_∞	239.77			239.77			239.77		
κ	00.13			00.13			00.13		
S	5			5			5		

	Model 2D – Temperature-dependent competition			Model 2E - Heatwave		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter						
K(SRL) Zone 1	7636.541	7634.873	7638.209	7393.082	7391.422	7394.742
K(SRL) Zone 2	8113.625	8111.946	8115.304	7862.029	7860.353	7863.705
K(SRL) Zone 3	6528.288	6526.608	6529.968	6335.981	6334.304	6337.658
K(SRL) Zone 4	10159.861	10158.189	10161.532	9885.260	9883.591	9886.928
K (ERL)/per zone	90.017			90.017		
M SRL (fixed)	0.00833			0.00833		
M ERL (fixed)	0.0058			0.0058		
h SRL (fixed)	0.7			0.7		
h ERL (fixed)	0.7			0.7		
Likelihood contributions						
Period	Value	sigma	q	Value	sigma	q
1	-181.537	0.231	2.26E-04	-159.979	0.259	2.28E-04
2	-174.788	0.236	2.12E-04	-156.535	0.261	2.15E-04
3	-165.688	0.251	5.96E-05	-142.524	0.284	6.02E-05
4	-103.748	0.347	4.22E-05	-87.254	0.379	4.26E-05
5	-137.468	0.292	1.26E-04	-117.589	0.324	1.27E-04
6	-97.781	0.361	1.02E-04	-80.214	0.396	1.03E-04
7	-148.844	0.268	2.79E-04	-137.246	0.285	2.81E-04
8	-196.915	0.210	2.54E-04	-183.179	0.227	2.55E-04
Total	-1206.670			-1064.400		
Fixed parameters						
Heatwave multiplier	1			1		
SRL F						
L_∞ Zone 1	107.4			107.4		
L_∞ Zone 2	107.4			107.4		

L_∞ Zone 3	127.39			127.39		
L_∞ Zone 4	147.79			147.79		
κ Zone 1	0.407			0.407		
κ Zone 2	0.407			0.407		
κ Zone 3	0.1701			0.1701		
κ Zone 4	0.3029			0.3029		
S Zone 1	9			9		
S Zone 2	9			9		
S Zone 3	10			10		
S Zone 4	4			4		
SRL M						
L_∞ Zone 1	122.28			122.28		
L_∞ Zone 2	122.28			122.28		
L_∞ Zone 3	178.12			178.12		
L_∞ Zone 4	184.26			184.26		
κ Zone 1	0.459			0.459		
κ Zone 2	0.459			0.459		
κ Zone 3	0.1390			0.1390		
κ Zone 4	0.2601			0.2601		
S Zone 1	5			5		
S Zone 2	5			5		
S Zone 3	7			7		
S Zone 4	3			3		
ERL						
L_∞	239.77			239.77		
κ	00.13			00.13		
S	5			5		

Table S5.3. Summary of Model 1 sensitivity parameter estimates and fixed inputs, where 'SRL F' indicates *Jasus edwardsii* females, 'SRL M' indicated *J. edwardsii* males and 'ERL' indicates *Sagmariasus verreauxi* (combined sexes). Changes to parameters are highlighted in bold.

	Model 1A – ISW growth sensitivity			Model 1A – Taroona growth sensitivity			Model 1A – High *M* sensitivity		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter									
K(SRL) Zone 1	4015.030	4013.306	4016.753	5560.815	5559.170	5562.460	8535.592	8533.786	8537.398
K(SRL) Zone 2	3673.499	3671.774	3675.224	8184.521	8182.852	8186.190	8996.582	8994.768	8998.395
K(SRL) Zone 3	5014.555	5012.827	5016.283	5608.284	5606.614	5609.953	7362.833	7361.015	7364.650
K(SRL) Zone 4	8533.885	8532.192	8535.578	9183.834	9182.172	9185.495	9667.258	9665.478	9669.039
K (ERL)/per zone	20. 086			20.086			20.086		
M SRL (fixed)	0.00833			0.00833			**0.0125**		
M ERL (fixed)	0.0058			0.0058			**0.0087**		
h SRL (fixed)	0.7			0.7			0.7		
h ERL (fixed)	0.7			0.7			0.7		
Likelihood contributions									
Period	Value	sigma	q	Value	sigma	q	Value	sigma	q
1	-128.533	0.306	3.24E-04	-174.340	0.240	2.77E-04	-166.459	0.250	2.09E-04
2	-121.043	0.316	3.05E-04	-169.834	0.243	2.61E-04	-157.573	0.259	1.98E-04
3	-108.118	0.341	8.58E-05	-160.061	0.259	7.34E-05	-140.057	0.288	5.60E-05
4	-55.192	0.451	6.07E-05	-100.773	0.353	5.20E-05	-83.515	0.387	4.01E-05
5	-75.582	0.406	1.81E-04	-136.020	0.294	1.55E-04	-112.316	0.334	1.21E-04
6	-52.804	0.459	1.41E-04	-98.834	0.358	1.24E-04	-73.407	0.411	9.76E-05
7	-112.903	0.326	3.95E-04	-142.160	0.278	3.40E-04	-144.057	0.275	2.55E-04
8	-150.537	0.270	3.58E-04	-194.728	0.213	3.10E-04	-188.061	0.221	2.32E-04
Total	-804.698			-1176.720			-1065.440		
Fixed parameters									
Heatwave multiplier	1			1			1		
SRL F									
L_∞ Zone 1	**112.28**			**132.41**			107.4		

L_∞ Zone 2	**112.73**			**107.4**			107.4		
L_∞ Zone 3	127.39			127.39			127.39		
L_∞ Zone 4	147.79			147.79			147.79		
κ Zone 1	**0.0978**			**0.1760**			0.407		
κ Zone 2	**0.0979**			**0.407**			0.407		
κ Zone 3	0.1701			0.1701			0.1701		
κ Zone 4	0.3029			0.3029			0.3029		
S Zone 1	**10**			**9**			9		
S Zone 2	**10**			**10**			9		
S Zone 3	10			10			10		
S Zone 4	4			4			4		
SRL M									
L_∞ Zone 1	**122.67**			**182.44**			122.28		
L_∞ Zone 2	**122.67**			**122.28**			122.28		
L_∞ Zone 3	178.12			178.12			178.12		
L_∞ Zone 4	184.26			184.26			184.26		
κ Zone 1	**0.3014**			**0.2279**			0.459		
κ Zone 2	**0.3015**			**0.459**			0.459		
κ Zone 3	0.1390			0.1390			0.1390		
κ Zone 4	0.2601			0.2601			0.2601		
S Zone 1	**7**			**4**			5		
S Zone 2	**8**			**8**			5		
S Zone 3	7			7			7		
S Zone 4	3			3			3		
ERL									
L_∞	239.77			239.77			239.77		
κ	00.13			00.13			00.13		
S	5			5			5		

	Model 1A – Low *h* sensitivity			Model 1D – Weak heatwave sensitivity			Model 1D – Strong heatwave sensitivity		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter									
K(SRL) Zone 1	7710.205	7708.559	7711.851	7678.657	7677.012	7680.303	7678.657	7677.011	7680.303
K(SRL) Zone 2	8417.768	8416.097	8419.439	8237.894	8236.223	8239.565	8276.703	8275.030	8278.376
K(SRL) Zone 3	6856.141	6854.469	6857.813	6663.499	6661.827	6665.171	6703.600	6701.926	6705.274
K(SRL) Zone 4	10664.759	10663.094	10666.424	10340.257	10338.592	10341.922	10277.373	10275.707	10279.040
K (ERL)/per zone									
M SRL (fixed)				0.00833			0.00833		
M ERL (fixed)				0.0058			0.0058		
h SRL (fixed)	**0.6**			0.7			0.7		
h ERL (fixed)	**0.6**			0.7			0.7		
Likelihood contributions									
Period	Value	sigma	q	Value	sigma	q	Value	sigma	q
1	-165.410	0.252	2.18E-04	-167.015	0.249	2.20E-04	-155.015	0.266	2.17E-04
2	-161.559	0.254	2.06E-04	-162.656	0.252	2.07E-04	-151.900	0.268	2.04E-04
3	-149.934	0.273	5.78E-05	-148.611	0.275	5.80E-05	-135.906	0.294	5.72E-05
4	-93.212	0.367	4.09E-05	-91.908	0.370	4.10E-05	-83.354	0.387	4.04E-05
5	-129.126	0.305	1.22E-04	-125.118	0.312	1.22E-04	-114.150	0.330	1.20E-04
6	-91.841	0.372	9.87E-05	-86.610	0.383	9.93E-05	-77.100	0.403	9.76E-05
7	-136.849	0.286	2.67E-04	-140.931	0.280	2.70E-04	-128.062	0.300	2.66E-04
8	-186.460	0.223	2.43E-04	-189.694	0.219	2.45E-04	-174.785	0.237	2.41E-04
Total	-1114.390			-1112.540			-1020.270		
Fixed parameters									
Heatwave multiplier	1			**1.1**			**1.5**		
SRL F									
L_∞ Zone 1	107.4			107.4			107.4		
L_∞ Zone 2	107.4			107.4			107.4		

L_∞ Zone 3	127.39			127.39			127.39		
L_∞ Zone 4	147.79			147.79			147.79		
κ Zone 1	0.407			0.407			0.407		
κ Zone 2	0.407			0.407			0.407		
κ Zone 3	0.1701			0.1701			0.1701		
κ Zone 4	0.3029			0.3029			0.3029		
S Zone 1	9			9			9		
S Zone 2	9			9			9		
S Zone 3	10			10			10		
S Zone 4	4			4			4		
SRL M									
L_∞ Zone 1	122.28			122.28			122.28		
L_∞ Zone 2	122.28			122.28			122.28		
L_∞ Zone 3	178.12			178.12			178.12		
L_∞ Zone 4	184.26			184.26			184.26		
κ Zone 1	0.459			0.459			0.459		
κ Zone 2	0.459			0.459			0.459		
κ Zone 3	0.1390			0.1390			0.1390		
κ Zone 4	0.2601			0.2601			0.2601		
S Zone 1	5			5			5		
S Zone 2	5			5			5		
S Zone 3	7			7			7		
S Zone 4	3			3			3		
ERL									
L_∞	239.77			239.77			239.77		
κ	00.13			00.13			00.13		
S	5			5			5		

Table 5.4. Summary of Model 2 sensitivity parameter estimates and fixed inputs, where 'SRL F' indicates *Jasus edwardsii* females, 'SRL M' indicated *J. edwardsii* males and 'ERL' indicates *Sagmariasus verreauxi* (combined sexes). Changes to parameters are highlighted in bold.

	Model 2B – High ERL(K) sensitivity			Model 2B – Low ERL(K) sensitivity			Model 2A – Low *h* (0.5) sensitivity		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter									
K(SRL) Zone 1	7641.124	7639.478	7642.770	7641.124	7639.478	7642.770	7641.124	7639.478	7642.770
K(SRL) Zone 2	8087.703	8086.033	8089.373	8087.703	8086.033	8089.373	8087.703	8086.033	8089.373
K(SRL) Zone 3	6544.629	6542.958	6546.300	6544.629	6542.958	6546.300	6544.629	6542.958	6546.300
K(SRL) Zone 4	10096.055	10094.390	10097.719	10096.055	10094.390	10097.719	10096.055	10094.390	10097.719
K (ERL)/per zone	**8103.080**			**20.086**			90.017		
M SRL (fixed)	0.00833			0.00833			0.00833		
M ERL (fixed)	0.0058			0.0058			0.0058		
h SRL (fixed)	0.7			0.7			**0.5**		
h ERL (fixed)	0.7			0.7			**0.5**		
Likelihood contributions									
Period	Value	sigma	q	Value	sigma	q	Value	sigma	q
1	-178.111	0.235	2.25E-04	-178.111	0.235	2.25E-04	-177.983	0.235	2.23E-04
2	-171.652	0.240	2.11E-04	-171.652	0.240	2.11E-04	-171.674	0.240	2.09E-04
3	-159.605	0.260	5.93E-05	-159.605	0.260	5.93E-05	-166.115	0.251	5.88E-05
4	-99.450	0.355	4.20E-05	-99.450	0.355	4.20E-05	-105.827	0.343	4.16E-05
5	-134.185	0.297	1.25E-04	-134.185	0.297	1.25E-04	-143.295	0.283	1.24E-04
6	-94.623	0.367	1.02E-04	-94.623	0.367	1.02E-04	-107.062	0.343	1.01E-04
7	-147.801	0.269	2.76E-04	-147.801	0.269	2.76E-04	-146.310	0.271	2.74E-04
8	-198.838	0.208	2.51E-04	-198.838	0.208	2.51E-04	-194.986	0.213	2.49E-04
Total	-1184.260			-1184.260			-1213.250		
Fixed parameters									
Heatwave multiplier	1			1			1		
SRL F									
L_∞ Zone 1	107.4			107.4			107.4		

L_∞ Zone 2	107.4			107.4			107.4		
L_∞ Zone 3	127.39			127.39			127.39		
L_∞ Zone 4	147.79			147.79			147.79		
κ Zone 1	0.407			0.407			0.407		
κ Zone 2	0.407			0.407			0.407		
κ Zone 3	0.1701			0.1701			0.1701		
κ Zone 4	0.3029			0.3029			0.3029		
S Zone 1	9			9			9		
S Zone 2	9			9			9		
S Zone 3	10			10			10		
S Zone 4	4			4			4		
SRL M									
L_∞ Zone 1	122.28			122.28			122.28		
L_∞ Zone 2	122.28			122.28			122.28		
L_∞ Zone 3	178.12			178.12			178.12		
L_∞ Zone 4	184.26			184.26			184.26		
κ Zone 1	0.459			0.459			0.459		
κ Zone 2	0.459			0.459			0.459		
κ Zone 3	0.1390			0.1390			0.1390		
κ Zone 4	0.2601			0.2601			0.2601		
S Zone 1	5			5			5		
S Zone 2	5			5			5		
S Zone 3	7			7			7		
S Zone 4	3			3			3		
ERL									
L_∞	239.77			239.77			239.77		
κ	00.13			00.13			00.13		
S	5			5			5		

	Model 2A – High *h* (0.8) sensitivity			Model 2C – Low *h* (0.5) sensitivity			Model 2C – High *h* (0.8) sensitivity		
Model Estimates	Value	90% Confidence Interval		Value	90% Confidence Interval		Value	90% Confidence Interval	
Parameter									
K(SRL) Zone 1	7612.143	7610.494	7613.792	7797.044	7795.285	7798.804	7528.115	7526.440	7529.791
K(SRL) Zone 2	7974.466	7972.795	7976.137	8646.414	8644.644	8648.185	7910.134	7908.449	7911.819
K(SRL) Zone 3	6469.797	6468.125	6471.469	6897.401	6895.625	6899.178	6377.937	6376.251	6379.623
K(SRL) Zone 4	9873.404	9871.739	9875.070	11095.557	11093.820	11097.293	9848.752	9847.076	9850.427
K (ERL)/per zone	90.017			90.017			90.017		
M SRL (fixed)	0.00833			0.00833			0.00833		
M ERL (fixed)	0.0058			0.0058			0.0058		
h SRL (fixed)	**0.8**			**0.5**			**0.8**		
h ERL (fixed)	**0.8**			**0.5**			**0.8**		
Likelihood contributions									
Period	Value	sigma	q	Value	sigma	q	Value	sigma	q
1	-176.768	0.237	2.25E-04	-179.277	0.234	2.20E-04	-180.766	0.232	2.30E-04
2	-170.414	0.242	2.11E-04	-172.898	0.239	2.06E-04	-174.052	0.237	2.16E-04
3	-156.765	0.263	5.94E-05	-170.127	0.245	5.80E-05	-163.341	0.254	6.06E-05
4	-97.056	0.360	4.21E-05	-109.128	0.337	4.11E-05	-101.640	0.351	4.30E-05
5	-130.646	0.303	1.26E-04	-144.903	0.281	1.23E-04	-134.388	0.297	1.28E-04
6	-90.620	0.375	1.02E-04	-108.852	0.340	9.98E-05	-94.158	0.368	1.04E-04
7	-147.062	0.270	2.77E-04	-144.630	0.274	2.72E-04	-148.776	0.268	2.83E-04
8	-197.979	0.209	2.51E-04	-189.584	0.219	2.47E-04	-197.212	0.210	2.58E-04
Total	-1167.310			-1219.330			-1194.180		
Fixed parameters									
Heatwave multiplier	1			1			1		
SRL F									
L_∞ Zone 1	107.4			107.4			107.4		
L_∞ Zone 2	107.4			107.4			107.4		
L_∞ Zone 3	127.39			127.39			127.39		

L_∞ Zone 4	147.79			147.79			147.79		
κ Zone 1	0.407			0.407			0.407		
κ Zone 2	0.407			0.407			0.407		
κ Zone 3	0.1701			0.1701			0.1701		
κ Zone 4	0.3029			0.3029			0.3029		
S Zone 1	9			9			9		
S Zone 2	9			9			9		
S Zone 3	10			10			10		
S Zone 4	4			4			4		
SRL M									
L_∞ Zone 1	122.28			122.28			122.28		
L_∞ Zone 2	122.28			122.28			122.28		
L_∞ Zone 3	178.12			178.12			178.12		
L_∞ Zone 4	184.26			184.26			184.26		
κ Zone 1	0.459			0.459			0.459		
κ Zone 2	0.459			0.459			0.459		
κ Zone 3	0.1390			0.1390			0.1390		
κ Zone 4	0.2601			0.2601			0.2601		
S Zone 1	5			5			5		
S Zone 2	5			5			5		
S Zone 3	7			7			7		
S Zone 4	3			3			3		
ERL									
L_∞	239.77			239.77			239.77		
κ	00.13			00.13			00.13		
S	5			5			5		

CHAPTER 6

General Discussion

General discussion

This thesis investigated the thermal tolerances of a local species, *Jasus edwardsii*, and a potentially range shifting species, *Sagmariasus verreauxi*, of spiny lobster in an ocean warming hotspot off south-east Australia. These thermal tolerances were then used to project future population change under climate change scenarios. There are several major findings that came from this thesis. Firstly, species performance across temperature differed between species, life stages and performance measures. This suggests that there is not a single measure of performance in these species of lobster that can accurately predict whole-organism changes under ocean warming scenarios. Secondly, individual measures of species performance do not reflect the relative competitive ability of the species, as indicated by the outcomes of competitive interactions over a range of temperatures. While individual thermal tolerances are useful tools in being able to predict changes to species under climate change scenarios, they are unlikely to accurately depict changes due to modification by behaviour. Finally, incorporating physiological mechanisms into models greatly affects projection estimates, with species interactions further complicating model outcomes. Incorporation of physiological tolerances in the Model of Intermediate Complexity for Ecosystem assessments (MICE) resulted in small changes in *J. edwardsii* projected biomass and large increases in *S. verreauxi* biomass. However, including competitive interactions resulted in larger and less predictable effects including decreases in *J. edwardsii* projected biomass. These results all indicate that factors influencing or driving species range shifts are complicated and not always immediately obvious. It also suggests that drivers of species range shifts may vary depending on ontogeny and specific ecosystem pressures faced by the species throughout their life history.

Thesis results

In Chapter 2, the thermal tolerance of a potentially range-shifting species at a critical larval stage was investigated across a range of temperatures. Using *S. verreauxi* puerulus, two measures of thermal performance were tested. Using intermittent-flow respirometry, metabolic rates were measured across a 10°C temperature range, as well as video recording of escape speeds exhibited by individuals across the same temperatures. It was found that puerulus stage *S. verreauxi* had different thermal optima for two different measures of species performance, indicating that a single measure could not accurately predict whole organism performance under future climate change scenarios. This supports recent studies that have found that aerobic scope is unable to predict whole organism performance in some species (Norin et al. 2014, Fitzgibbon et al. 2017). The thermal optima of both measures were above the current temperatures experienced in Tasmania, suggesting that with future ocean warming in Tasmania, *S. verreauxi* has the capacity to increase in individual measures of performance and hence positively influence range extension potential and population growth in Tasmania.

In Chapter 3, the previous study was extended to include a local species of lobster, *J. edwardsii*, as well as another life stage (juvenile) to investigate interspecific and ontogenetic differences in performance between the two species. Using the same methods from the previous study (intermittent-flow respirometry for metabolic rates and escape speed videos), it was found that thermal optima differed between species, life stages and measure of performance. In addition, while *S. verreauxi* had higher thermal optima for escape speed, *J. edwardsii* had overall higher magnitudes of response, suggesting further that a single measure of performance may not accurately predict whole-organism response at the individual or species level (Norin et al. 2014, Fitzgibbon et al. 2017). There was difference in thermal tolerances between puerulus and juvenile stages of both species, suggesting that environmental pressures for both species may change during ontogeny, reflected in changes in optima of difference performance measures

(Sinclair et al. 2016). As *S. verreauxi* had higher thermal optima than *J. edwardsii*, they have the capacity to increase in performance with future ocean warming in Tasmania. However, this may not be to the detriment of the *J. edwardsii* population, as although *J. edwardsii* has lower thermal tolerance optima, these optima are still below temperatures predicted to be reached by 2100 (Stobart et al. 2016). However, temperature projections did not account for marine heatwaves which are likely to increase in frequency and magnitude in the future (Oliver et al. 2017, Oliver et al. 2018), which may actually increase temperatures above those optimal for *J. edwardsii*, particularly in the north of the state.

Chapter 4 investigated the effect of temperature on food competition between adult stage *J. edwardsii* and *S. verreauxi*. The competitive ability of *J. edwardsii* to secure the food item was maintained above temperatures that were found to be optimal for other measures of performance. Adult *J. edwardsii* were significantly more aggressive and active than *S. verreauxi*, which were more submissive and inactive. This suggests that aggressive behaviour likely benefits food acquisition, even at temperatures above those determined optima. Aggressive behaviour has been observed in other crustaceans as key determinant in interaction outcome for resources (Kaiser et al. 1998, Tran et al. 2014). Aggressive behaviour also increased in a resident snapper species when exposed to range-shifting con-specifics, allowing the species to remain resilient and competitive to the new species in the area (Marshak & Heck 2017). These studies and the current results suggest that *J. edwardsii* may be competitively resilient to the range-shifting *S. verreauxi* in Tasmania. If this is the case, with continued warming, it is likely that *S. verreauxi* might undergo a range contraction towards the northern, equatorward extent of its range (Fitzgibbon et al. 2014). If this species is then competitively excluded from being able to extend its range and increase in abundance in Tasmania, it may instead be compressed into a smaller range at intermediate temperatures and latitudes. This study also revealed that individual measures of performance do not necessarily predict the

indirect outcomes of species interactions. Thermal optima for both species did not match the outcome of the food competitive interactions, supporting previous work that showed that using just physiological mechanism were not able to fully encompass changes the marine community (Lord et al. 2017). Therefore, while individual thermal tolerance data is informative, caution should be used when applying species thermal tolerances as predictors for species range shifts in isolation of species interactions (Lord et al. 2017).

In Chapter 5, physiological and competitive performance data from the previous chapters were incorporated into a MICE. It was found that incorporating physiological data greatly affected the model biomass predictions under future climate changes scenarios. For *J. edwardsii*, incorporating physiological data into the model resulted in decreases in projected biomass due to temperatures being below those optimal of the species, even in the next 30 years. Alternatively, for *S. verreauxi*, biomass increased significantly with the inclusion of physiological parameters, suggesting that even small increases in water temperatures will positively influence species abundance and population growth at this advancing end of its distribution. There had been a recent push to include physiological mechanisms into predictive models as they may more accurately predict changes as a result of climate change than purely correlative models (Kearney & Porter 2009, Evans et al. 2015). This MICE highlights the clear differences between model outputs when including and excluding physiological data in the model, and hence the importance of including such data where its available to increase predictive accuracy.

Introducing the effect of competition in the model resulted in unexpected results. Despite *J. edwardsii* being more competitive at higher temperatures, it appeared that the physiological thermal tolerance of *S. verreauxi* outweighed this, resulting in projected increases in *S. verreauxi* biomass in the future while *J. edwardsii* projected biomass decreased. Based on individual thermal tolerances measures and competitive interaction outcomes, this would not

have been an expected result. Another aspect to highlight about this study is the effect on projected biomass of both species as a result of simulated marine heatwave conditions. Heatwave simulations increased biomass of both species, although to different extents. In models including just physiological data, heatwave simulations increased biomass of both species, significantly so for *S. verreauxi*. In models that included competitive ability, heatwave simulations mitigated the negative affect of competition in *J. edwardsii*, while again greatly increasing biomass for *S. verreauxi*. These results only hold true for moderate heatwave simulations, low and high intensity simulations resulted in decreased biomass for *J. edwardsii* and a smaller increase in biomass for *S. verreauxi*. This increase in complexity has been observed in experimental trials where outcomes predicted by physiological mechanisms were modified by species interactions and their indirect effects (Lord et al. 2017). Overall, this chapter highlights the importance of including both physiological and interspecific interaction data into projection models, especially when indirect effects of species interactions may not be immediately obvious (Kearney & Porter 2009, Evans et al. 2015).

Limitations and future research

There are several limitations of this study that should be noted. Firstly, in Chapters 2 and 3, only thermal tolerances of puerulus and juvenile stage lobsters were investigated. This provides information on only part of the life history of spiny lobsters. Due to variation observed between the two life stages examined, it could be expected that other life stages, such as the planktonic larval phyllosoma or adult life stages would also exhibit different thermal tolerances to those observed in Chapters 2 and 3. Previous work in insects has observed differences in tolerances between life stages (Kingsolver et al. 2011, Sinclair et al. 2016) and therefore investigating other life stages would provide a more comprehensive understanding of how species thermal tolerances may change through their ontogeny.

There were only two measures of performance investigated in Chapters 2 and 3, aerobic scope and escape speed. As the results showed there was significant variation between the two measures, with evidence from other physiological studies (Norin et al. 2014, Fitzgibbon et al. 2017), it would be safe to assume that other measures of performance on the same species may have different thermal tolerances and optima also. Therefore, investigating the effect of temperature on additional performance measures would be valuable in furthering our understanding of how temperature affects different organismal processes and how these changes affect overall species performance. Some of these measures to be examined could include growth, feed intake and assimilation, reproduction and activity rates.

One major limitation of the studies conducted in Chapters 2 and 3 is the use of cultured puerulus and juveniles of *S. verreauxi* and comparing their thermal tolerances to those of wild-caught *J. edwardsii*. While this limitation was unavoidable due to the very low numbers of *S. verreauxi* pueruli obtained from puerulus collectors in Tasmania, conclusions drawn from comparing a species reared in a relatively thermally stable environment and not exposed to interspecific competition or predation with one that has been exposed to these influences, are tentative. It could be assumed that the *J. edwardsii* collected from the wild are those with performance traits more strongly selected for than reared *S. verreauxi*. However, apart from high variation in some recovery measures, the relative variation among and between the two species appeared to be relatively similar. This suggests that, as long as caution is used to interpret the results of these studies, valid conclusions and assumptions can be made based on the data collected. However, as recruitment of *S. verreauxi* puerulus in Tasmania is predicted to increase with future changes to ocean currents and temperatures (Cetina-Heredia et al. 2015), there could be opportunities to expand these studies using wild-caught *S. verreauxi* puerulus and juveniles in Tasmania, strengthening the predictive potential of the data.

In addition to examining only two life stages in Chapter 3, the competition experiments from Chapter 4 were only conducted for adult stage lobsters. Here, investigating the competition between puerulus and juveniles would have been extremely valuable in determining changes in competitive ability during ontogeny. As it is likely that the introduction of *S. verreauxi* into Tasmania is through larval dispersal (Cetina-Heredia et al. 2015), investigating the competition between larval and juvenile stages for food across current and future temperatures would provide valuable insight into how successful the species may be in its extension in Tasmania.

Another limiting factor on Chapter 4 was the used of some berried *J. edwardsii* females. As the two species have different biological attributes, including size at maturity, *J. edwardsii* females were smaller and yet mature compared to *S. verreauxi* at similar size that were not yet sexually mature (Montgomery 1992, Gardner et al. 2006). Berried females have been observed to be more aggressive in other crustacean species (Campbell 1990, Mello et al. 1999) and this likely had an effect on the observed results. While there was no difference in the number of wins between male and female *J. edwardsii* in the study (indicating that there wasn't a significant effect of the females being berried and the species as a whole was competitive) it would be interesting to conduct the same experiments at a time of year when neither species is spawning to determine competitive strength not affected by reproduction. In addition to a different time frame, it would be interesting to determine if sex, size, and different numbers of individuals of both species affects the outcome of competitive interactions (i.e Williams et al. 2009, Matheson & Gagnon 2012, Greggor & Laidre 2016).

While food competition is an important and informative indicator of species competitive ability, it is likely that the *J. edwardsii* and *S. verreauxi* will also compete for other resources such as habitat and shelter (Booth 2006, Jeffs et al. 2013). The puerulus stage of spiny lobsters are an active, but non-feeding stage in the life cycle (Phillips et al. 2006). It could be assumed that for this particular life stage, competitive ability in terms of avoiding predators and finding suitable

habitat and shelter to settle into are more important than food acquisition. Therefore, investigating the competitive interaction for shelter resources in all life stages, particularly the younger stages, would provide insight on how competitive ability changes during ontogeny, as well as how competitive strength for difference resources, i.e. food versus shelter, may change through the species life stages.

The studies conducted in Chapters 2-4 all had relatively short temperature acclimation periods. While short acclimation periods could be used to determine effects of short-term extreme heating events such as marine heatwaves, the results in this thesis may be less applicable to address long-term effects where long-term acclimation and physiological plasticity may mitigate the negative effects of ocean warming (Johnson & Bennett 1995, Temple & Johnston 1998, Camacho et al. 2006, Donelson et al. 2011, Schulte et al. 2011, Grigaltchik et al. 2012, Grenchik et al. 2013, Foo & Byrne 2016).

In some of the temperature treatments in Chapters 2 and 3, there were relatively few replicates. Due to sampling constraints for *J. edwardsii* puerulus and supply constraints for *S. verreauxi* juveniles, some of the temperature treatments had fewer replicates, resulting in less robust estimates of some of the measure of performance. While this limitation was unavoidable, longer experimental periods and adjusted experimental design could be implemented in future.

All ecological implications from this thesis were developed from laboratory experiments. While controlled experiments are valuable ways to investigate effects of change on species, they may not capture true species behaviour in wild conditions. In addition to lab-based investigations of escape speed and competition, field-based data could also be collected. In terms of escape speed, stereo-filmed interactions between lobsters and their predators would provide insight into fight or flight scenarios. As lobsters were forced to react in lab conditions, they may instead rely on cryptic behaviour more often than active predator escape mechanisms

(Phillips et al. 2006). In terms of competitive interactions, again filming interactions for food could be performed in natural conditions using baited underwater cameras.

The MICE developed in Chapter 5 addresses the competitive interaction between the species, however other species interactions such as predation could not be included in the current study. Including new interactions in a limited food web would illustrate how the two spiny lobster species interact within their environment with other species. In addition to expanding the model, it would be very valuable to combine the modelling approach used above with those of others, for example oceanographic models of puerulus settlement for more accurate modelling outputs of *S. verreauxi* biomass in Tasmania (i.e. estimates from Cetina-Heredia et al. (2015)).

Other future research should include effects of ocean acidification. Ocean warming is not occurring in isolation, and not considering effects of ocean acidification on marine species may not accurately encompass all changes observed (Hoegh-Guldberg & Bruno 2010, Doney et al. 2012). Lobsters have been shown to be negatively affected by ocean acidification through increased disease susceptibility and decreased growth (Small et al. 2015, Rato et al. 2017, McLean et al. 2018). Investigating the effects of ocean acidification on all life stages of *J. edwardsii* and *S. verreauxi*, in isolation and in conjunction with temperature trials, will again provide a more robust understanding of current and future potential changes, increasing our predictive ability and aiding potential adaptive management of resources. To date, there are very few ocean acidification studies on spiny lobster species. This is a large gap in our understanding and filling this would provide much needed knowledge of effects of future acidification on lobster species that are commercially, socially and ecologically valuable.

Conclusion

Overall, thermal tolerances and model outcomes suggest that *S. verreauxi* will expand its range further into Tasmania and increase in abundance in the future as a result of ocean warming. While thermal tolerances of *J. edwardsii* physiology and competitive strength suggest that the species will continue to perform well and be competitively advantaged compared to *S. verreauxi* in the near future, modelled outcomes suggest that with an increase in *S. verreauxi* abundance, *J. edwardsii* may be disadvantaged as a result of strong positive temperature influences on *S. verreauxi* in the future. This result may be somewhat mitigated by future simulated heatwave events, as heatwaves may have a positive influence on biomass projections of both species though positive influences of increased temperature on individual performance and hence population growth.

In conclusion, species' range shifts in response to ocean warming are likely facilitated or hindered by a range of different physiological mechanisms, dependent on species, life stage and pertinent ecological pressures. In addition to the array of potential drivers, species interactions are introducing unexpected and complicated indirect effects. Teasing apart which mechanisms may be the most influential for facilitating or hindering range shifts, and hence predicting future shifts, will require a comprehensive understanding of the effects of temperature on different performance measures at different life stages of interacting species, as well as a clear understanding of potential environmental stressors.

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